Development of chironomid-based transfer functions for surface water quality parameters and temperature, and their application to Quaternary sediment records from the South Island, New Zealand

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Contents

ABSTRACT

This thesis resulted in the development of robust chironomid-based transfer-functions for February mean air temperature and the concentration of total nitrogen (TN) in lake-water. The New Zealand transfer-functions for both variables compare favourably with chironomid-based transfer-functions for equivalent variables from elsewhere in the world, and diatom-based transfer-functions for nutrients and lake production from New Zealand. The application of the temperature and TN transfer-functions provided insight into New Zealand climate conditions during the last glacial and served as validation for the reconstructions.

Chironomid-based Temperature reconstructions from lake silts preserved in the banks of Lyndon Stream indicate a maximum cooling of ca 4 ºC between 26.6 and 24.5 ka BP, which is consistent with estimates based on beetles and plant macrofossils. A cooling of 4 ºC is insufficient to explain the lack of canopy tree pollen in many New Zealand pollen records at this time. Other environmental parameters additional to temperature may have limited the expansion forest cover.

The chironomid-based TN reconstructions infer a trend of rapidly deteriorating water-quality in a small doline in north-west Nelson, in the South Island of New Zealand following deforestation immediately surrounding the lake ca. 1970 AD. The overall trend and timing of eutrophication inferred from the chironomids was consistent with other biological proxies and actual observations of changes in lake water quality.

The chironomid-based transfer-functions provide a valuable new tool for the study of long-term climate variability and improving our understanding of the response of aquatic ecosystems to long-term natural and human induced environmental change in New Zealand lakes. I have identified some possibilities for future research which should improve the performance of these transfer-functions. The improvement of the chironomid taxonomy and the expansion of the training set should be the highest priorities.

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

CHAPTER 7

CHAPTER 8

LIST OF TABLES

CHAPTER 2

CHAPTER 3

CHAPTER 4

CHAPTER 5

CHAPTER 6

CHAPTER 8

CHAPTER 1 INTRODUCTION

1.1 GENERAL INTRODUCTION

The Dipteran family Chironomidae (non-biting midges) is the most widely distributed and frequently the most abundant group of insects in freshwater (Armitage et al., 1995). Taxon abundance, coupled with short life cycle duration, makes this group an ideal target for use in paleolimnological studies (Walker, 1995; Walker, 2001). The chitinous head-capsules of the larval stage are resistant to decay and are therefore frequently preserved in lake sediments. As such, chironomids have been used extensively in the Northern Hemisphere in paleoenvironmental research to reconstruct climate change and to quantify the effects of human impact on lake ecosystems (e.g. Brooks and Birks, 2000; 2001; Brooks et al., 2001; Quinlan and Smol, 2002).

Paleoenvironmental analysis using chironomids is sparse in New Zealand, consisting of early qualitative work (Deevy, 1955) and some later more quantitative efforts (Boubee, 1983; Schakau, 1986; 1991; 1993) that attempted to determine the ecological tolerances of the New Zealand chironomid taxa. None of the earlier New Zealand investigations resulted in the production of quantitative inference models. Information derived from lake classification and ordination was applied to down-core chironomid fossil data, but the modern ecological results were applied qualitatively. Furthermore, the studies by both Boubee and Schakau were limited either by altitude and/or the length of the nutrient gradient covered by the 'training set'. Neither of the studies collected chironomid remains from lakes situated above the tree-line (~ 1000 to 1300 m a.s.l.). Since those studies were completed, there has been major progress in the use of statistics in paleoecological research, and a major improvement in the resolution of the taxonomy of the New Zealand chironomid taxa, particularly the Orthocladiinae (Boothroyd, 1994; 1999; 2002; 2004). Despite these developments, there has been no attempt to develop chironomid-based inference models to enable the quantitative reconstruction of past environmental conditions.

The main aim of this Ph.D. thesis is to develop New Zealand chironomid-based transfer functions as a tool to study past climate change and to quantify the human impact on New Zealand aquatic ecosystems, in particular lake nutrients or productivity. The impetus for this work comes from two sources:

Firstly, New Zealand paleoclimate history has become a focus for international studies, because New Zealand is seen as a good distal location to test paleoclimate hypotheses developed from Northern Hemisphere data (e.g. Broecker, 1997). This is particularly true for the time interval from the last glacial maximum (LGM) (c. 21,000 years ago) to the start of the present interglacial (c. 13,000 years ago). Many studies of glacial systems (e.g. Denton and Hendy, 1994; Shulmeister et al., 2005) and biotic indicators, notably pollen (e.g. McGlone et al., 2004; Vandergoes and Fitzsimons, 2003) have been undertaken to investigate these changes but are limited by inadequate or contradicting estimates of temperature change.

Recently, there has been a focus on developing new quantitative paleoclimate tools for use in New Zealand. Transfer functions have been developed for phytoliths (Prebble et al., 2002) and testate amoebae (Wilmshurst et al., 2003) while bioclimatic modelling approaches have been applied to beetles (e.g. Marra, 2002; Marra et al., 2004; 2006). For some of these proxies (e.g. phytoliths) the inference of climate parameters from the data is not straightforward, while with others (e.g. testate amoeba) reconstructions appear to be affected by preservation biases. New, high resolution and widely applicable proxies are needed to test patterns of inferred climate change. Studies in the Northern Hemisphere have shown that even though chironomids are aquatic invertebrates, they can be used to reliably infer past air temperatures, and hence track climate change (e.g. Lotter et al., 1997; Brooks and Birks, 2000). Hence, the development of a proxy for air temperature for a southern latitude land mass (New Zealand) will lead to the acquisition of critical data concerning climate change in this region during the Late Quaternary.

Secondly, there is growing concern in New Zealand about damage to waterways from changed agricultural practices (notably dairying in dry-land areas) and urbanisation. Even though a relatively small percentage of the lakes in New Zealand can be classified as eutrophic (22%) or hypertrophic (18%) (Taylor and Smith, 1997), local councils have initiated ‘long-term’ water quality monitoring programmes (e.g. Burns and Rutherford, 1998) and developed strategies and targets to facilitate the restoration of ‘damaged’ ecosystems (e.g. Hamilton, 2003; Rutherford, 2003). However, rigorous scientific monitoring of lakes and estuaries in New Zealand only extends back as far the early 1980s (Taylor and Smith, 1997) and there are few continuous records of physical and chemical parameters. Therefore it is difficult to establish base-line levels for lake productivity and set reasonable targets for lake restoration in the absence of long-term records.

Many studies in the Northern Hemisphere have successfully used transfer-functions based on biological proxies (e.g. chironomids and diatoms) to extend lake records beyond historical time. These long-term paleolimnological records (in tandem with other proxies, e.g.: palynomorphs)

provide valuable information on the natural functioning of lake/catchment systems and their response to anthropogenic disturbance (deforestation and intensive farming) (e.g. Bennion and Appleby, 1999; Brooks et al., 2001; Kauppila et al., 2002; Quinlan and Smol, 2002; Langdon et al., 2006). At this stage there is only one other robust published transfer function that is capable of quantifying past lake production (chlorophyll *a*) in New Zealand (Reid 2005). Reid (2005) also produced diatom-based transfer functions for total phosphorus (TP) and dissolved reactive phosphorus (DRP), but these did not perform as well as the chlorophyll *a* transfer function. The addition of a second, chironomid-based transfer function for lake nutrients or productivity will allow comparison and cross validation between the chironomid and diatom-based transfer functions.

1.2 RESEARCH OBJECTIVES

The two main aims for this Ph.D. project are to:

1. Develop quantitative inference models (transfer-functions) for environmental variables based on the abundance of chironomid head-capsules preserved in modern lake sediments, and

2. Apply the resulting robust transfer-functions to dated lake records. In order to achieve these goals this thesis addresses the following 5 objectives, with relevant chapters in parentheses.

Part 1. Model development

(i) Develop a dataset of modern New Zealand chironomid assemblages from lakes spanning large temperature and productivity gradients (4).

(ii) Use multivariate statistical techniques to explore the main environmental controls on the abundance and distribution of the New Zealand chironomid taxa in this modern dataset (4 & 5).

(iii) Construct quantitative inference models (transfer-functions) for environmental variables that are responsible for the greatest amount of statistically significant variation in the modern chironomid assemblages (6).

Part 2: Model application

(i) The most robust chironomid-based transfer-function for temperature will be applied to a lake record from the late Otiran glacial sequence (LOGS). A site was selected that would enable the testing of the temperature transfer function against other proxies (plant macrofossils and beetles) and also provide useful climate data for this time period. (7)

(ii) The most robust chironomid-based transfer-function for lake nutrients or productivity will be applied to a recent (< 1000 cal yrs BP) lake record to quantify changes in trophic status (chlorophyll *a*, total phosphorous, total nitrogen) in response to human activities in the catchment (e.g. deforestation and farming practices). A site will be selected that will enable the comparison of the pattern of eutrophication produced by the chironomid reconstructions with actual observations of lake conditions. (8)

A pilot study will also be performed to test the potential for the use of chironomids as a proxy for anthropogenic eutrophication in New Zealand brackish lakes and lagoons. (3)

Another major objective of this thesis is to establish a reliable taxonomy for the sub-fossil chironomid larvae of New Zealand. There have been recent developments in the taxonomy of this group in New Zealand (e.g Boothroyd, 1994; 1999; 2002; and Martin & Forsyth, unpublished data). However, the taxonomy of the modern taxa is based on both head-capsule morphology and features that are not preserved in the fossil record.

1.3 INTRODUCTION TO RESEARCH METHODS

As mentioned in the previous section, there are two main parts to this project, **Part 1** (model development) and **Part 2** (model application). The following section provides a brief outline of the main techniques that were used to achieve the research objectives outlined in **Section 1.2**. A diagrammatic representation of the process of transfer function development and application is depicted in **Fig. 1.1.**

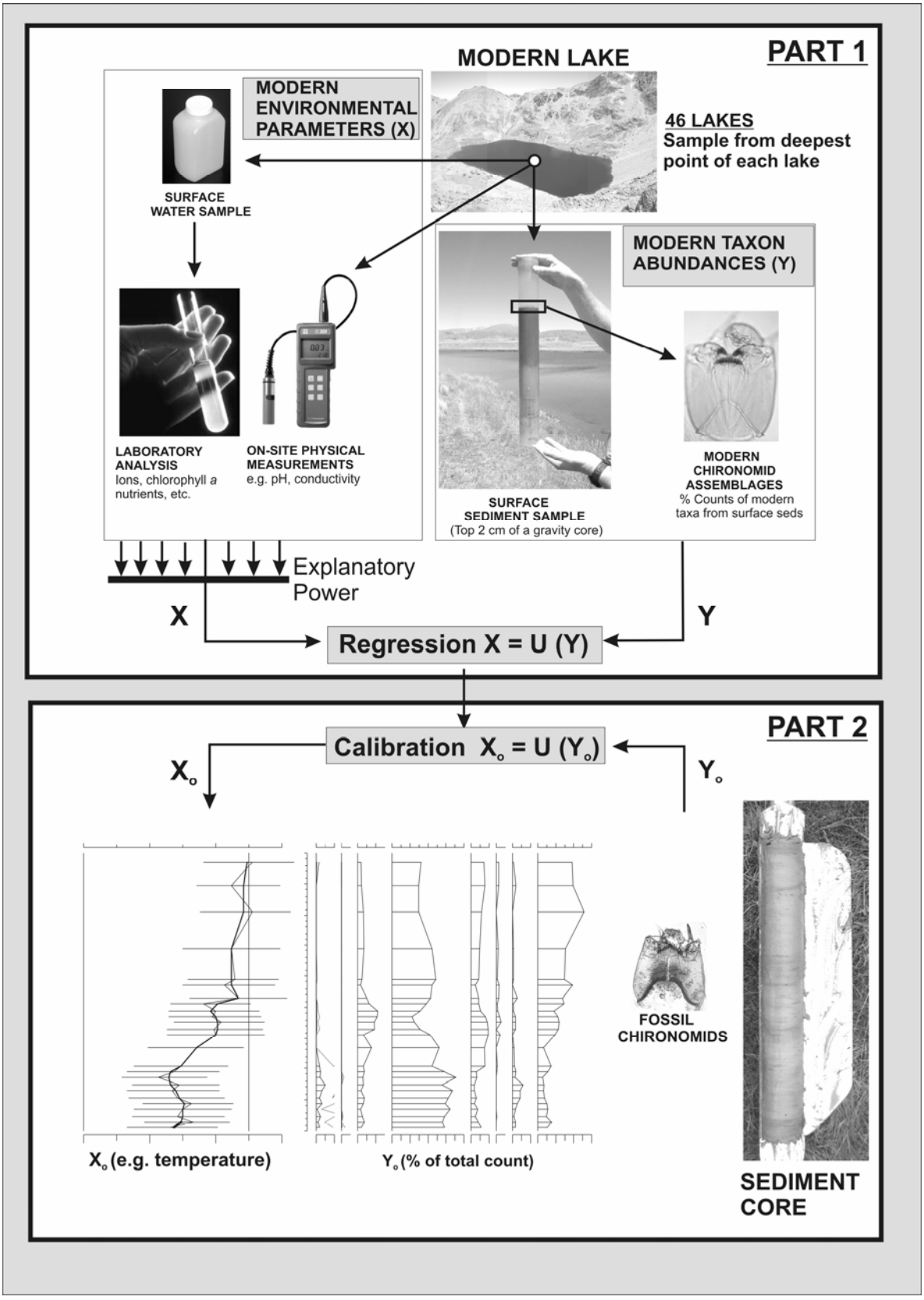


Fig. 1.1: Schematic representation of the research methods used to achieve the main research objectives for Part 1, model development, and Part 2 model application.

Part 1: Model Development

Exploratory data analysis

This project uses a suite of well-established numerical techniques to develop chironomid-based quantitative inference models (transfer-functions). The basic methodology was developed by Imbrie and Kipp (1971) and requires the development of a large dataset ('training set') of:

a. Taxon abundances (hereafter denoted by **Y**): In this case the relative abundances (% of total number of individuals from each site) within defined spatial and temporal domains, i.e.: chironomid abundances from surface sediments from individual lakes, representing a limited amount of time (**Fig. 1.1**). This is important as we have to be certain that the measured environmental parameters (part (ii)) correspond to the same period of time represented by the surface sediment chironomid assemblage.

b. Values for environmental variables (hereafter denoted by **X**): (e.g. water temperature, pH, conductivity etc) for each lake (**Fig. 1.1**).

Assuming that our chironomid assemblages are representative of both **a)** the chironomid fauna of the entire lake and **b)** a similar time period to that represented by the environmental parameters, the next step uses multivariate statistical methods (constrained ordinations, e.g. canonical correspondence analysis (CCA)) to determine which environmental parameter(s) explain the greatest amount of variation in the modern chironomid species data. Transfer-functions will only be attempted for these environmental variables (**Fig. 1.1**). Constrained ordinations are also used to determine the nature of species turnover with respect to the main explanatory variables, i.e. are taxon responses linear or unimodal?

Model development

A transfer-function relates X and Y through an empirical calibration function (hereafter denoted U. Two common approaches can be used to determine the the value of U, these are called the "classical" and "inverse" regression approaches (Osborne, 1991), i.e:

(1) $Y = U(X)$ the "classical" approach

(2) $X = U(Y)$ the "inverse regression" approach

The "inverse regression" approach is most commonly used to develop transfer functions for one particular environmental variable, based on taxon abundance data. The "inverse regression" approach considers each environmental variable individually, because a multivariate regression reduces to a series of multiple regressions of individual dependent variables (ter Braak 1995). Multivariate regression using partial least squares (PLS) or weighted-averaging partial least squares (WA-PLS) is commonly used to model linear and unimodal species responses of the modern species (Y) to the modern environmental parameter (X).

An unknown value of X (X_o) can now be estimated directly from the modern regression equation ((1) above) based on the known abundances of taxa represented in the fossil record (Y_o) (**Fig. 1.1**), i.e.:

(3) $X_o = U(Y_o)$

Part 2: Model application

Lake sediments will be collected by coring a lake or sampling outcrop that will produce a record that spans the required time period (for both temperature and human impact studies) and come from a lake that has experienced recent, human-induced eutrophication (for the human impact study). Isotopic dating (^{14}C, ^{210}Pb, ^{137}Cs and ^{239}Pu) will be used to provide age constraints on these lake records.

The remains of chironomids (the resistant chitinous head-capsules) will be extracted from lake sediments using a well-established sediment processing technique (e.g. Walker, 2001). These head-capsules will be identified and counted. The resulting head-capsule counts (Y_o) will be used to reconstruct either temperature or the target proxy for anthropogenic eutrophication (X_o) using computer software designed specifically for this purpose.

The chironomid-based reconstructions will be compared with other biological proxies when they are available including palynomorphs and plant macrofossils.

1.4 THESIS OUTLINE

The structure of this thesis is largely constrained by the two main objectives of this study (see section 1.2), i.e. it outlines the methodology and results of the transfer-function development (Part A), and presents a number of case studies where the successful transfer functions have been applied to particular records with specific aims in mind (Part B). **Chapter 3** also presents the results of a multi-proxy study (chironomids, pollen, foraminifera, etc.) from Lake Forsyth, a hypertrophic, brackish coastal lake from the South Island, New Zealand. This study was performed prior to the development of the chironomids-based transfer-functions. Therefore the biological proxies provide only qualitative environmental inferences in this case.

Some of the material presented here has already been published (most of the contents of **Chapters 3, 4, 5, 6,** and **7** see **Appendix D**). Generally papers are required to be more concise, and consequently contain less detail than it is possible to include in a thesis chapter. Therefore, some details that were left out of the papers have been included in the chapters of this thesis. Some of the data were also reconsidered and modified *after* the manuscripts were accepted for publication. This is largely due to the fact that new taxonomic information has led to the development of a more robust transfer-function for lake trophic status (see discussion on chironomids taxonomy in **Chapter 2**).

This thesis comprises nine chapters:

Chapter One provides a general introduction to the development and application of chironomids and other quantitative paleo-environmental indicators internationally and in New Zealand, and discusses the necessity for this study. This chapter also outlines the research objectives, methods, and provides a thesis outline.

Chapter two discusses the current state of the taxonomy of chironomids larvae in New Zealand. A brief description of all 51 taxa enumerated in the development of the training set is provided. Some observations by the author regarding some contentious morphotypes (i.e. the genus *Chironomus* and the tribe Macropelopini) are also discussed. Details of the diagnostic features used to identify all of the 51 taxa and figures are also provided in **Appendix A**; an identification key for the New Zealand fossil Chironomidae larvae.

Chapter Three presents the methodology, results and discussion of a multi-proxy study of the environmental history of Lake Forsyth (Te Wairewa) from south of Banks Peninsula in the South Island of New Zealand.

Chapter Four presents the methodology for the exploratory data analyses which will determine the main drivers of chironomid distribution in New Zealand lakes

Chapter Five presents results for these exploratory data analyses and a discussion of their implications

Chapter Six presents the results and discussion of the transfer-function development

Chapter Seven. Presents the methodology, results and discussion of the application of the temperature transfer-function to a lake record spanning the MIS 3/2 transition (26.6 -24.5 ka BP)

Chapter Eight presents the methodology, results and discussion of the application of the lake productivity (trophic level index (TLI)) transfer-function to a recent (<100 years BP) record of Lake Alexander from north-west Nelson in the South Island of New Zealand.

Chapter Nine presents a synthesis of the preceding chapters and comments on the problems and potential for future studies in this field.

Acknowledgements

References

Appendix A

Identification key for the New Zealand sub-fossil Chironomidae.

Appendix B

Complete limnological and catchment data for the New Zealand lake dataset.

Appendix C

Supplementary tables from the exploratory numerical analyses in Chapter 4 and 5

Appendix D

Papers published and accepted to international peer-reviewed journals.

Woodward C. A, Shulmeister J. (2005). A Holocene record of human induced and natural environmental change from Lake Forsyth (Te Wairewa), New Zealand. *Journal of Paleolimnology* **34**: 481-501.

Woodward C. A., Shulmeister J. (2006). New Zealand chironomids as proxies for human-induced and natural environmental change: Transfer functions for temperature and lake production (chlorophyll *a*). *Journal of Paleolimnology* **36**: 407- 429.

Woodward C. A., Shulmeister J. (in press). Chironomid-based reconstructions of summer air temperature from lake deposits in Lyndon Stream, New Zealand spanning the MIS 3/2 transition. *Quaternary Science Reviews.* Available online 9 August 2006. doi:10.1016/j.quascirev.2006.06.004.

Appendix E

Data disc containing Microsoft® Excell spreadsheets with supplementary data, including raw chironomid head-capsule counts from the training set and pollen counts.

CHAPTER 2 NEW ZEALAND CHIRONOMID TAXONOMY

2.1 INTRODUCTION

The Dipteran family Chironomidae (non-biting midges) is the most widely distributed and frequently the most abundant group of insects in freshwater (Armitage et al., 1995). Like all Diptera, chironomids are holometabolus and undergo a complete metamorphosis including larval, pupal and adult (imago) life stages (**Fig. 2.1**)

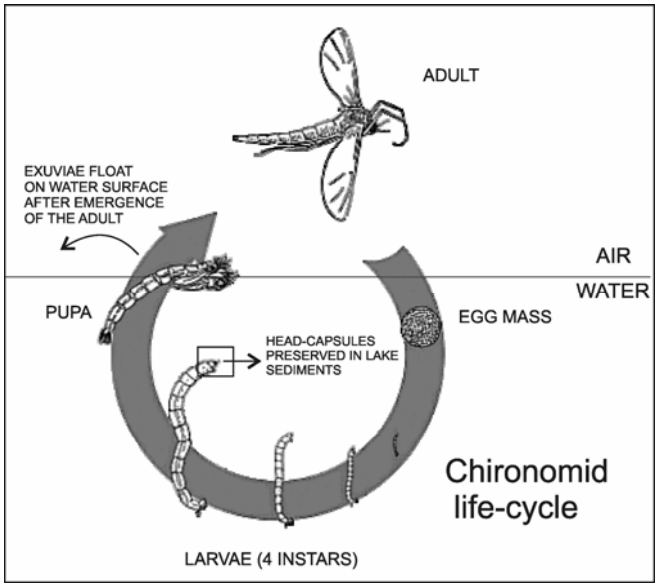


Fig. 2.1: The chironomid life-cycle.

The chitinous head-capsule of the larvae is the element that is most commonly preserved in lake sediments (**Fig. 2.1** and **2.2a** and **b**), although exuviae (the remains of the pupal stage, **Fig. 2.1**) and adults were occasionally encountered in recent (Holocene) sediments during this study. The family Chironomidae can be divided into ten sub-families (Cranston, 1995). Chironomid taxa described from New Zealand belong to six of these sub-families: Tanypodinae, Chironominae, Orthocladiinae Podonominae, Diamesinae and Telmatogetoninae (Boothroyd, 2000). The New Zealand chironomid fauna comprises three main elements: common cosmopolitan genera (with northern-hemisphere affinities, mainly belonging to Chironominae, Orthocladiinae, and Tanypodinae), genera restricted to the southern hemisphere (belonging to the Podonominae and Diamesinae) and endemic genera (Winterbourn, 1980). Five endemic genera have been described from New Zealand: *Maoridiamesa* Brundin, *Lobodiamesa* Pagast, *Zealandochlus* Brundin, *Gressittius* Sublette & Wirth (formally *Anatopynia*, Hudson), and *Paucispinigera* Freeman.

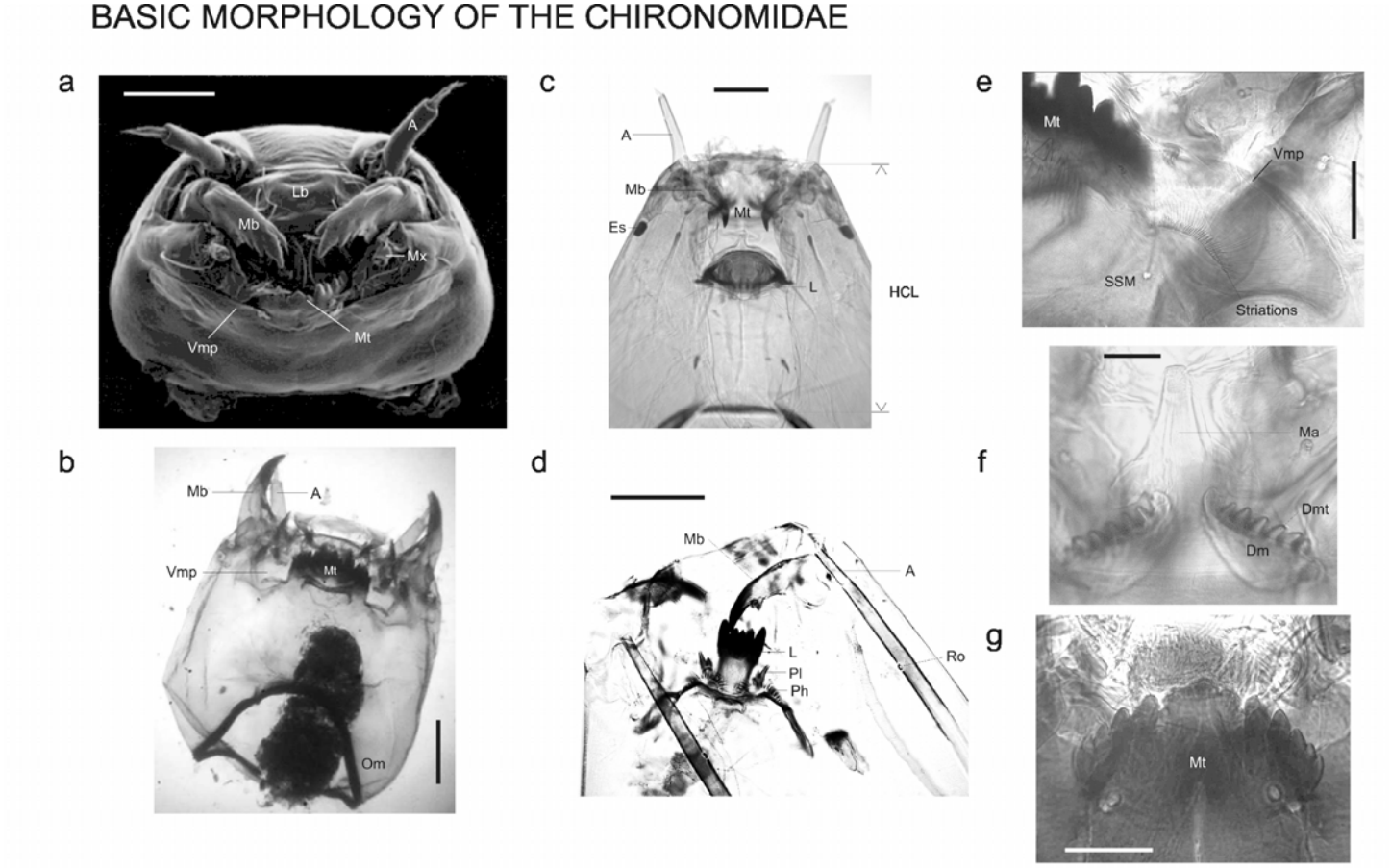


Fig 2.2: Basic morphology of living and sub-fossil chironomid head-capsules. a) SEM image, all others transmission light microscope images. All images from slide mounts of living material except for d).
a) SEM image of *Chironomus* head-capsule (from living material) b) *Chironomus* head-capsule c) Tanypodinae head-capsule (Macropelopini) d) *Ablabesmyia* (Tanypodinae)
e, f, and g. Menta from Chironominae, Tanypodinae, and Diamesinae. The menta of Diamesinae,Orthocladiinae and Podonominae lack the well developed ventromental plates (Vmp) present in the Chironominae. Scale bars are 100 µm for a,b,c and d; 25 µm for e,f, and g.
Abbreviations are: A = antenna, Dm = dorsomentum, Dmt = dorsomental teeth, Es = eye spot, L = ligula, Lb = labrum, Mb = mandible, Mt = mentum, Mx = maxilla
Om = occipital margin, Ph = pectin hypopharyngis, Pl = paraligula, Ro = ring organ, SSM = sub-mental seta

Currently 130 taxa (including unplaced and un-described species) have been reported from New Zealand (Boothroyd, 2000). Only a small proportion of these taxa have been collected as living larvae from New Zealand lakes. Timms (1982) collected a total of 16 profundal chironomid taxa during his study of 20 South Island lakes, and reported a maximum number of 8 taxa from three lakes (Rotoiti (Nelson), Marymere, and Gault). The remaining 17 lakes had an average of 4.7 taxa. The samples taken by Timms (1982) probably underestimate the true taxon richness because of a bias towards profundal taxa. Stark (1981) found a total of 17 chironomid taxa associated with the macrophytes in the littoral zone of Lake Grasmere.

It is common practice to sample surface sediment samples (< 2 cm sediment depth) from the deepest point each lake to provide an indication of the presence and abundance of chironomid taxa when developing modern ecological datasets. Previous studies from elsewhere in the world (e.g. Brodersen and Lindegaard, 1997) have demonstrated that these samples provide an assemblage that is representative of all the chironomid taxa either living in the lake, or in some cases, in streams or rivers that flow into it. The total number of taxa found in these assemblages can frequently be greater than the number reported as living larvae collected from various habitats within each lake. Schakau (1993) reported a total of 37 different taxa from the surface sediments of the 35 New Zealand lakes sampled as part of her PhD thesis, while in this study 51 chironomid taxa were recovered from surface sediment samples from 46 New Zealand lakes (**Table 2.1**).

The total number of taxa encountered in New Zealand surface sediment samples is comparable to many other similar studies in the Northern Hemisphere (e.g. Lotter et al. 1997, 1999; Olander et al., 1999). However, unlike many studies from the Northern Hemisphere, it appears that the New Zealand fauna is dominated by only 20 common taxa (present in abundances ≥ 2% in at least 2 lakes) (Schakau, 1993 and this study). This could be a true reflection of the presence of ubiquitous monotypic taxa in New Zealand; however it seems more likely that this is an illusion created by the current state of the taxonomy of the larval life stage in this country.

Recently, there has been considerable progress in the refinement of the taxonomy of the New Zealand chironomids, particularly from the sub-family Orthocladiinae (Boothroyd, 1994; 1999; 2002; 2004; Boothroyd and Cranston, 1995). However, there are still many New Zealand chironomid species that are based on descriptions of the adult stage (e.g. *Chironomus zealandicus* Hudson) and connections between the various life stages (larvae, pupae, and adult) are incomplete (Boothroyd, 2000). Consequently, for many of the New Zealand genera (e.g. *Chironomus*, *Polypedilum*, *Parochlus*) or even tribes (e.g. Macropelopini) many adult specimens have been described and formally named while the larvae can only be confidently identified to the level of genus or tribe. Further work is required to collect and rear larvae from these taxa to

No.	Taxon Name	Taxonomic Reference
1	*Ablabesmyia mala*	Hutton (1902b)
2	*Camptocladius stercorarius*	De Geer (1776)
3	*Chironomus* spp.	Meigen (1803)
4	*Cladopelma curtivalva*	Kieffer (1917a)
5	*Corynocera* Undescribed sp.	Stark (1971)
6	*Corynoneura scultellata*	Winnertz (1846)
7	*Crictocopus* spp.	Wulp (1874)
8	*Crictocopus aucklandensis*	Sublette and Wirth (1980)
9	*Crictocopus hollyfordensis*	Boothroyd (2002)
10	*Crictocopus planus*	Boothroyd (1990)
11	*Crictocopus zealandicus*	Freeman (1959)
12	*Eukiefferiella brundini*	Boothroyd and Cranston (1995)
13	*Eukiefferiella insolida*	Boothroyd
14	*Eukiefferiella* spp.	Thienemann (1926)
15	*Harrisius pallidus*	Freeman (1959)
16	*Hevelius carinatus*	Sublette and Wirth (1980)
17	*Kaniwhaniwhanus chapmani*	Boothroyd (1999)
18	*Kiefferulus opalensis*	Forsyth (1975)
19	*Larsia* sp.	Fittkau (1962)
20	Tribe Macropelopini (Undifferentiated)	
21	*Maoridiamesa* spp.	Pagast (1947)
22	*Naonella kimihia*	Boothroyd (2004)
23	*Naonella forsythi*	Boothroyd (1995)
24	*Naonella* "305"	Unofficial morphotype
25	Orthoclad sp. A "High Rise"	Undescribed Boothroyd (2000)
26	Orthoclad sp. I	Unofficial morphotype
27	Orthoclad sp. B "Tongue"	Undescribed Boothroyd (2000)
28	Orthoclad sp. C "Claspers"	Undescribed Boothroyd (2000)
29	Orthoclad sp. G	Unofficial morphotype
30	Orthoclad sp. 1/6	Unofficial morphotype
31	Orthoclad sp. J	Unofficial morphotype
32	Orthoclad sp. D "Pear"	Undescribed Boothroyd (2000)
33	Orthoclad sp. E	Unofficial morphotype
34	*Paratrichocladius pluriserialis*	Freeman (1959)
35	*Parachironomus cylindricus*	Freeman (1959)
36	*Paratanytarsus grimmii*	Schneider (1885)
37	*Parochlus* spp.	Enderlein (1912e)
38	*Paucispinigera* sp.	Undescribed sp. Stark (1971)
39	Tribe Pentaneurini (Undifferentiated)	
40	*Pirara matakiri*	Boothroyd and Cranston (1995)
41	*Podochlus* spp.	Brundin (1966)
42	*Podonomus* spp.	Philippi (1865)
43	*Polypedilum* spp.	Undescribed sp. Boothroyd
44	*Pseudochironomus* sp.	Saether (1977)
45	*Smittia verna*	Hutton (1902)
46	*Stictocladius* sp.	Edwards (1931c)
47	*Tanytarsus* spp.	Wulp (1874)
48	*Tanytarsus funebris*	Freeman (1959)
49	*Tanytarsus vespertinus*	Hutton (1902)
50	*Xenochironomus canterburyensis*	Freeman (1959)
51	*Chironomus* sp. a	Martin & Forsyth (unpublished data)

Table 2.1: Taxon names (and references) for the 51 chironomid taxa recovered from the surface sediment samples from the New Zealand 46 lakes sampled in this thesis.

confidently link the identity of the larvae to a pre-existing formally named adult stage. Jon Martin and Don Forsyth (unpublished data) have taken a different approach with regards to the problematic genus *Chironomus*.

They have identified nine distinct karyotypes (based on chromosomes from the salivary glands) and have developed preliminary taxonomic keys.

A further problem lies in the identification of sub-fossil or fossil material, which is most commonly based on the morphology of the head-capsule, particularly the mentum (**Fig. 2.2**) and (in the case of the Chironominae) the ventromental plate (**Fig. 2.2e**). Whereas traditional identification of many species relies on the morphology of the abdomen, specifically the terminal segments (anal tubules and procercus **Fig. 2.9**); these parts are not commonly preserved in the fossil record. Even many of the chitinous structures from the head-capsule (structures from the labrum and epipharynx, antennae, mandibles (**Fig. 2.2**)) are lacking in many fossil specimens .

The main aim of this chapter is to describe the taxonomic nomenclature used in this thesis, and to outline the major taxonomic developments since the work of Boubee (1983) and Schakau (1986, 1991, 1993). I will also focus on the most recent developments with the taxonomy of the genus *Chironomus* (Martin and Forsyth unpublished data) and discuss problems with the current classification of the tribe Macropelopini. These two taxa were the most common taxa in the surface sediment samples (especially *Chironomus*) so the resolution of the taxonomy of these two groups is extremely important. This discussion will include the presentation of observations made by the author during the course of this study. These observations were based on the data gathered from sub-fossil head-capsules from the surface sediment samples, and live material collected from many of the lakes in the sample set. Full details of the preparation of the sub-fossil and live chironomid material is provided in **Chapter 4 Section 4.3**.

Each of the five sub-families (Tanypodinae, Chironominae, Orthocladiinae Podonominae, and Diamesinae) collected during this study will be discussed separately. A complete list of the 51 taxa recovered from the surface sediments is listed in **Table 2.1**. In depth descriptions will only be provided were taxa are considered to be new morphotypes, otherwise I will refer to the original taxonomic reference. An identification key for the New Zealand fossil Chironomidae is provided in **Appendix A**.

2.2 TANYPODINAE

Tribe Macropelopini

Boothroyd (2000) lists 9 described species belonging to the tribe Macropelopini from New Zealand. All 9 species have been described in their adult form, but only one, *Gressittius antarcticus* Sublette and Wirth (formally *Anatopynia antarctica* Hudson) has been formally described in its larval form and associated with the pupal and adult (imago) life stages (Freeman,

1959). The genus *Gressittius* was first erected by Sublette and Wirth (1980). Although very similar in many respects to other genera belonging to the tribe Macropelopini, Sublette and Wirth distinguished this genus in the adult form from *Macropelopia* by the lack of a mesonotal tubercle, and from *Apsectrotanypus* due to the lack of mesopleural and mesosternal setae, by r-m intersecting M distal to m-cu, and by the claws being digitate rather than pointed.

Schakau (1993) differentiated the Macropelopini larvae into three types, based on the number of teeth on the dorsomentum (**Fig. 2.2f** and **Fig. 2.3a & b**). Head-capsules with 4-5, 6, and 7-8 teeth on each dorsomental plate were identified as *Apsectrotanypus*, *Gressittius antarcticus* and *Macropelopia* respectively. Both Forsyth (1971) and Stark (1981) depict the larvae of *G. antarcticus* with 6 large teeth and one smaller accessory tooth (**Fig. 2.3a**). Fittkau (1962) mentions the number of teeth on the paralabial comb (= dorsomental plate) as a diagnostic feature separating the larvae of *Apsectrotanypus* and *Macropelopia*:

Apsectrotanypus Fittkau
"Kopf dunkelbraun, Körper braun, gelblich marmoriert. Palpus maxillaris doppelt so lang wie breit. Paralabialkämme mit 5 Zähnen"

Head dark brown, body yellow and mottled. Palpus maxillaris twice as long as it is wide. Paralabial comb with 5 teeth.

Macropelopia Thienemann
"Kopf gelbrot, Körper blutrot. Palpus maxillaris viermal so lang wie breit. Paralabialkämme mit 7 (-8) Zähnen"

Head yellowish red, body blood red. Maxillary palp four times as long as it is wide. Paralabial comb with 7 (-8) teeth.

It therefore seems reasonable to assign Macropelopini head-capsules to these genera based on the number of teeth on the dorsomentum alone. However, identification of the Macropelopini head-capsules based on the number of teeth on the dorsomentum alone is likely to be unreliable if we cannot be sure whether we are dealing with 3rd or 4th instar larvae. It was observed during this study that the number of teeth on the dorsomentum increases during larval development. Macropelopini larval head-capsules from 53 individuals from the surface sediments of Lake Mackenzie were examined to test the relationship between head-capsule length and the number of dorsomental teeth. The length of the head-capsule was measured from the post-occipital

margin to anterior margin as depicted in **Fig. 2.2c**. A large number of pupae were also collected using a sweep net from the water surface of Lake Mackenzie at the time the surface sediment sample was collected. These all possessed the thoracic respiratory trumpet that is characteristic of *G. antarcticus* (**Fig. 2.6 a & b**).

As it was expected the number of teeth on the dorsomentum increased with respect to head-capsule length. A trend line was fitted to an X-Y 'scatterplot' of head-capsule length versus the number of dorsomental teeth in Excel® (**Fig. 2.4**). The fitted logarithmic curve possessed an excellent predictive power (r^2= 0.81) suggesting that the number of teeth on the dorsomentum is related to larval development. The smaller head-capsules with 4-5 dorsomental teeth (**Fig. 2.3c** and **d**) look identical to the larvae tentatively associated with the pupae of *Macropelopia umbrosa* by Stark (1981). Given their small size it is highly likely that these head-capsules are early instar Macropelopini larvae.

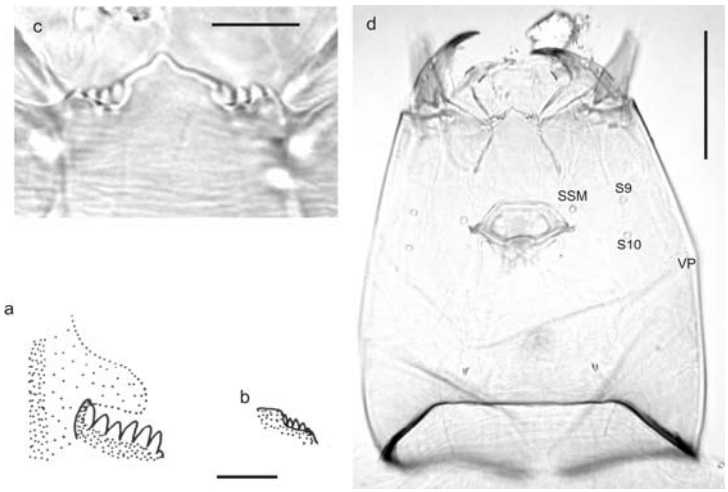


Fig. 2.3: Teeth on the dorsomentum of **a)** *Gressittius antarcticus* and **b)** ? *Macropelopia umbrosa* as identified and depicted by Stark (1981). **b)** is more likely to be an early instar belonging to the tribe Macropelopini. Both **c** and **d** depict the dorsomentum and setae pattern from a small (100 µm long) head-capsule from Lake Mackenzie with an identical dorsomentum. Scale bars are 20 µm for **a** and **b** and **c**, 40 µm for **d**. Abbreviations for setae identical to those used in **Fig. 2.5**.

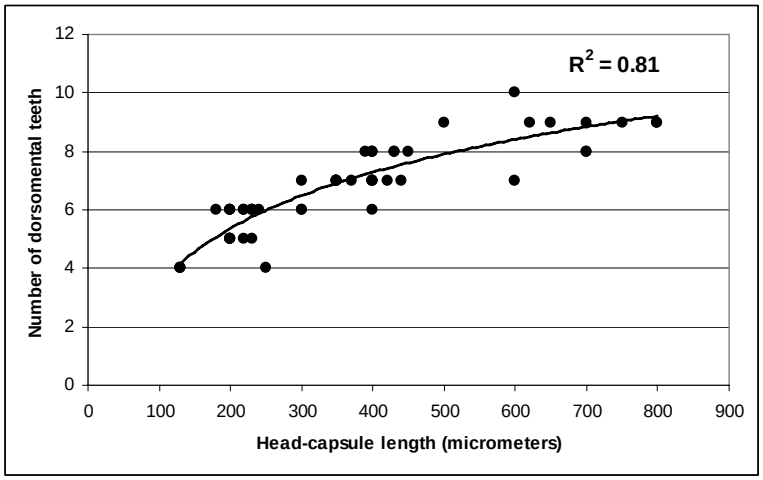


Fig. 2.4: The relationship between the head-capsule length and the number of teeth on the dorsomentum from 53 head-capsules belonging to the tribe Macropelopini from the surface sediments of Lake Mackenzie. A logarithmic curve has been fitted and the r^2 is displayed

Rieradevall and Brooks (2001) have also observed that the number of teeth increases on the dorsomentum during the larval development of the Macropelopini. Rieradevall and Brooks argue that cephalic setation patterns provide a much more reliable method for the identification of sub-fossil head-capsules belonging to the sub-family Tanypodinae. The characteristic pattern of the dorsal and ventral cephalic setal pockets and pores (**Fig. 2.5**) show relatively little intrageneric variation between larval instars or species, or across zoogeographic regions (Rieradevall and Brooks, 2001).

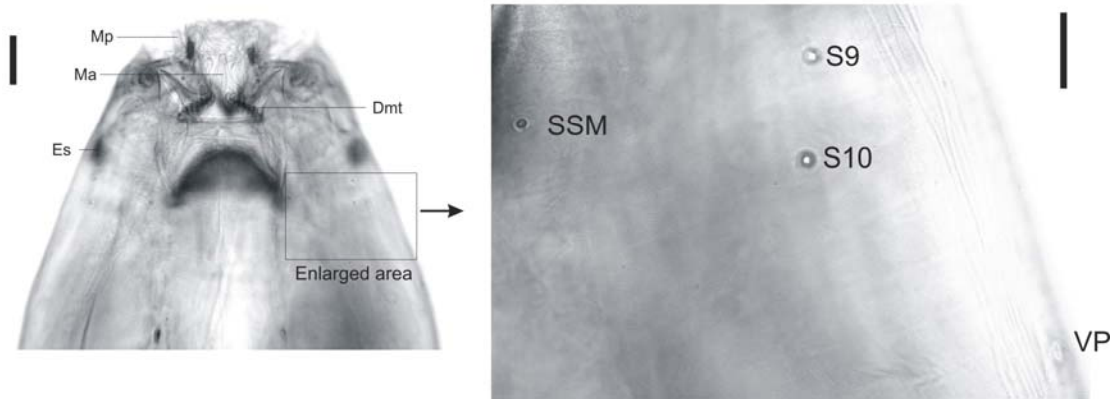


Fig. 2.5: Ventral cephalic setation from the tribe Macropelopini. Abbreviations as in **Fig. 2.2** except for: SSM (sub-mental setae) and VP (ventral pore). Scale bar = 90 μm on the left and 25 μm in the enlarged view.

I also investigated the division of the Macropelopini head-capsules into different morphotypes using the cephalic setation. A *Gressittius antarcticus* pupa was found with the larval cuticle (thoracic segments and head-capsule) still attached, and was possibly preserved in the early stages of ecdysis (moulting) (**Fig. 2.6a**) This provided a positive association between the pupa and the larval stages. The pupa was identified as *G. antarcticus* by the characteristic thoracic respiratory trumpet (**Fig. 2.6b**). The setation pattern for *G. antarcticus* is depicted in **Fig. 2.6c** and **Fig. 2.8 number 1**. The S9 and the S10 were slightly anterior to the submental seta (SSM), with the ventral pore (VP) posterior to the SSM. The dorsal pore (DP), S7 and S8 were posterior to the S5. This setation pattern is similar to the setation pattern described by Rieradevall and Brooks (2001) for *Apsectrotanypus*. The S9 and S10 are situated only slightly anterior to the SSM of *G. antarcticus* while the S9 and S10 are well forward of the SSM of *Apsectrotanypus*.

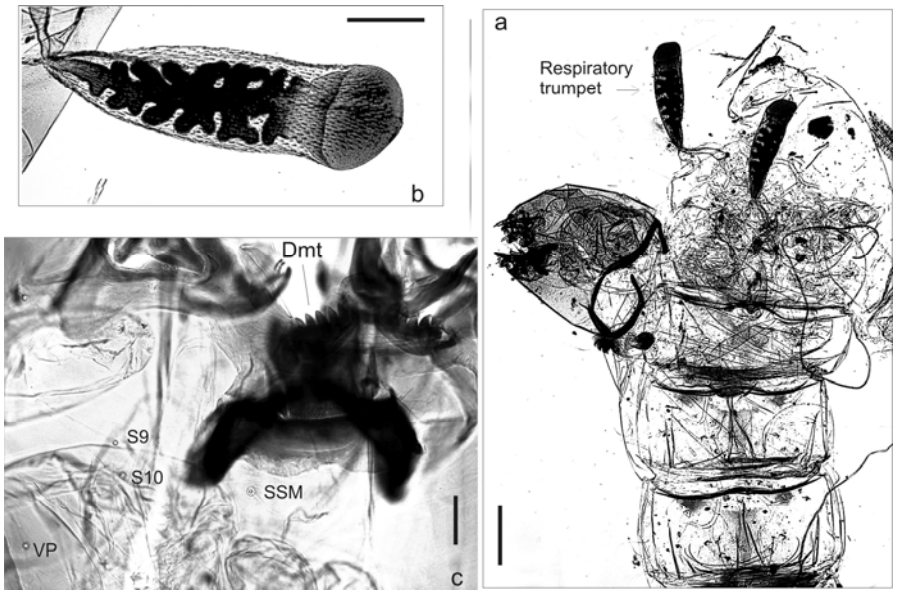


Fig. 2.6: a) *Gressittius antarcticus* head-capsule associated with pupa. **b)** Enlarged view of respiratory trumpet with characteristic convoluted trachea. **c)** Ventral cephalic setation from the head-capsule. Scale bars **a)** 300 µm **b)** 60 µm **c)** 25 µm

279 sub-fossil head-capsules and 10 mounted whole larval specimens from 20 lakes were then examined to see if there is any variation in the setation patterns of the New Zealand Macropelopini. The length of the head-capsule was also measured using the same method as described previously for the investigation into larval tooth development (**Fig. 2.2c**). Four major setation patterns were found (**Fig. 2.8**). The main difference between these patterns was the location of the S9 and S10 relative to the SSM. Within these categories there were slight variations with the S9 or S10 being closer to or further away from the SSM. It is difficult to say at this stage if all of these actually correspond to a different taxon. Despite the fact that Rieradevall and Brooks (2001) state that there is little variation in the setation patterns between instars the fact that some patterns (especially setae pattern 6) are limited to the early instars suggests that the S9 and S10 may migrate forwards during larval development.

Four of the Setae types; 1, 2, 4 and 5 exist across a wide range of head-capsule sizes and may therefore actually represent individual taxa. Setae pattern number 1 corresponds to *G. antarcticus*, while 2 is very similar to the setae pattern of *Apsectrotanypus* (as depicted by Rieradevall and Brooks, 2001) with the S9 and S10 located further forward from the SSM (Fig. 2.8). Setae patterns 4 and 5 are most similar to the setae patterns of *Macropelopia* as depicted by Rieradevall and Brooks (2001). Differential compression or folding of the chitin in poorly preserved material may effect the orientation of the S9 and S10 relative to the SSM.

The data for all of the aforementioned counts can be found in **Spreadsheet E1** the supplementary data disc (**Appendix E**).

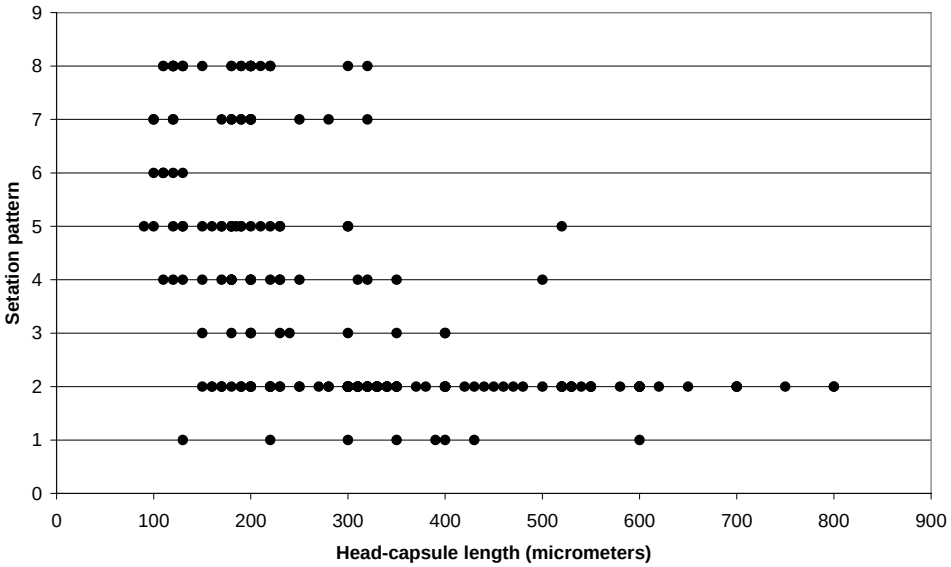


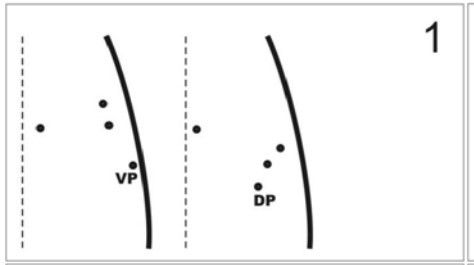
Fig. 2.7: Relationship between head-capsule length and the type of ventral cephalic setation. Setation numbers refer to the types depicted in Fig. 2.8.

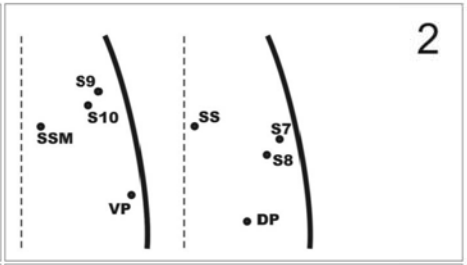
Since the chironomid training set uses all of the instars in the development of the inference models, the number of dorsomental teeth can not be considered a reliable method for distinguishing between different Macropelopini taxa. Further work is also required to develop the cephalic setation patterns as a reliable method for identification of this tribe. The evidence provided here suggests that there is variation in the cephalic setation patterns in the New Zealand Macropelopini. However, future work should focus on:

1. separating larvae into karyotypes, then associating these karyotypes with setation patterns, or
2. linking larval stages to positively identified adult stages (as with *G. antarcticus*) then associating a setation pattern with this taxon. This could be achieved by rearing live larvae and examining the shed head-capsules after emergence of the imago.

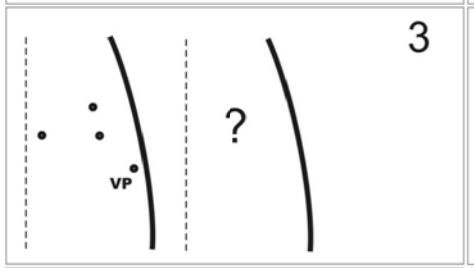
Until this work is performed, I have adopted a conservative approach with the Macropelopini in the modern New Zealand chironomid training set. All head-capsules with teeth on the dorsomentum (**Fig. 2.5**; **Fig. 4**, **Appendix A**), have been identified as Macropelopini. In some cases the dorsomentum may become detached from the head-capsule. The Pentaneurini can be distinguished from the Macropelopini by the presence of spinules on the head-capsule (as in *Ablabesmyia* **Fig. 3**, **Appendix A**) and the shape and position of the ventral pore (VP). It was observed during the course of this study that all the New Zealand Pentaneurini possess a VP that is an ellipsoid (not circular) and is located anterior of the SSM (**Fig. 3 Appendix A**).

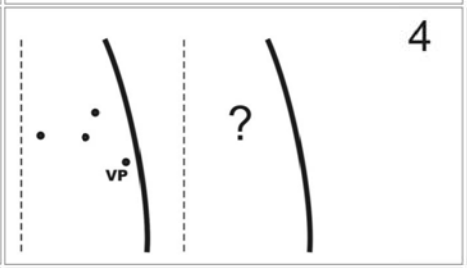
MACROPELOPINI SETAE PATTERNS

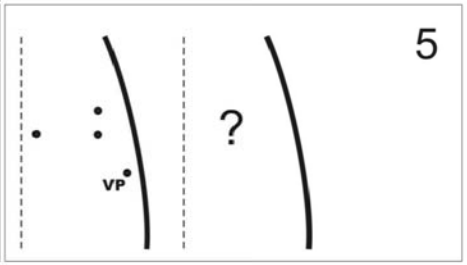




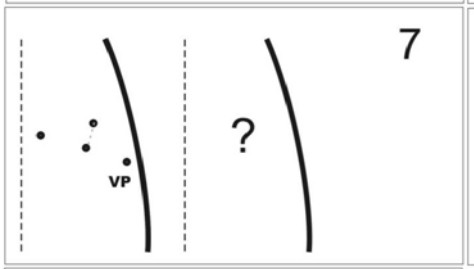
S9 and S10
anterior to the SSM

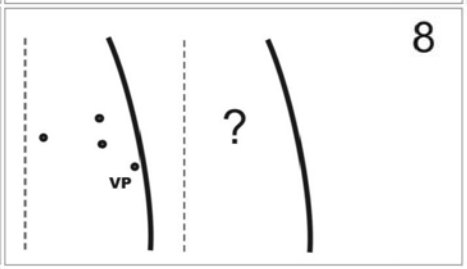




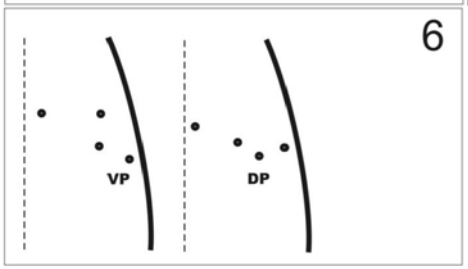


S10 in line with
SSM





SSM in between
S9 and S10



SSm anterior to S9

Fig.2.8: Setation patterns for the Macropelopini from 279 sub-fossil head-capsules and 10 mounted whole larvae from 20 lakes. Each pattern is numbered from 1 to 8. The setae patterns have been divided into four main groups dependent on the relative position of the 4 ventral setae.

Tribe Pentaneurini:

Stark and Winterbourn (2000) in their key for the New Zealand Chironomidae distinguish *Ablabesmyia mala* from other Pentaneurini by the presence maxillary palps with more than one basal segment (**Fig. 6, Appendix A**). These more delicate structures rarely preserve in the sub-fossil and fossil material. The cephalic setation (**Fig. 3, Appendix A**) ligula and pectin hypopharayngis (**Fig. 5, Appendix A**) are useful diagnostic features for identifying sub-fossil material. The ligula is darkly pigmented with 5 teeth (two larger outer teeth 3 smaller inner teeth). The middle of the inner three teeth is slightly smaller than the outer two. The pectin hypopharayngis consists of ca. 20 elongate teeth orientated radially from the base (**Fig. 5, Appendix A**). At least one undescribed species, and one other described species (*Zavrelimyia harrisi* Freeman (formerly *Pentaneura*) occur in streams and lakes in New Zealand (Stark and Winterbourn 2000) (**Fig. 7, Appendix A**). Elongate tanypod head-capsules with spinules (**Fig. 3, Appendix A**) lacking any of the diagnostic features (e.g. ligula, setation obscured) where identified to the level of tribe only (Pentaneurini). Two head-capsules with a ligula resembling the genus *Larsia* Fittkau were found in the surface sediments of Lake Mackenzie and Lake Mason. The outer teeth on the ligula of Australian species of *Larsia* are approximately the same length as the inner teeth (Cranston unpublished data). The two head-capsules identified as *Larsia* possessed teeth of approximately equal length on the ligula (**Fig. 8, Appendix A**). *Larsia* has not been previously described from New Zealand before and this assignment requires further investigation.

No head-capsules belonging to the genus *Zavrelimyia* were found in the surface sediment samples during this study. The ligula, pectin hypopharayngis and paraligula as depicted by Forsyth (1971) distinguish this genus from *Ablabesmyia mala* (**Fig. 7, Appendix A**).

2.3 CHIRONOMINAE

The taxonomic key of Stark and Winterbourn (2000) enabled the identification of most of the sub-fossil head-capsules belonging to this sub-family. Head-capsules belonging to 14 taxa, including 11 genera, were found in the surface sediments of the training set (**Table 2.1**). Stark and Winterbourn (2000) provide a key for 15 taxa. This includes 13 out of the 14 taxa encountered during this study, and two genera (*Microtendipes* and *Cryptochironomus*) that were not found in the 46-lake training-set. Head-capsules belonging to the sub-family Chironomidae are distinctive because of the presence of well developed ventromental plates (**Fig. 2.2b and e**)

(except for *Harrisius pallidus* , **Fig. 27**, **Appendix A**). *Kiefferulus opalensis*, *Parachironomus* sp., *Xenochironomus* sp., *Cladopelma curtivalva*, *Chironomus* spp., *Polypedilum* spp., *Paucispinigera* sp. and *Pseudochironomus* sp. possess broad flattened ventromental plates (**Fig. 13**, **14**, **15**, **16**, **20**, **22**, **21**, and **23** in **Appendix A** respectively). The number and position of the teeth on the mentum and the presence of serrations on the outer margin on the ventromental plate (**Fig. 12, Appendix X**) are useful features for identifying these taxa. *Harrisius pallidus* (**Fig. 27**, **Appendix A**) possesses a concave mentum, with inconspicuous ventromental plates.

Corynocera sp., *Paratanytarsus*, *Tanytarsus vespertinus* and *Tanytarsus funebris* possess more elongate ventromental plates (**Fig. 11**, **Appendix A**). The pigmentation of the central tooth (**Fig. 25** and **26**, **Appendix A**) and the presence of notches or a trifid central tooth (**Fig. 25** and **26**, **Appendix A**) are useful characteristics for distinguishing between *Paratanytarsus*, *Tanytarsus vespertinus* and *Tanytarsus funebris* (**Fig. 25a**, **25b**, **26a** and **b**, **Appendix A** respectively). *Corynocera* sp. is characterised by the possession of 3 teeth on the mentum (**Fig. 24**, **Appendix A**). Stark and Winterbourn (2000) mention three species belonging to the genus Chironomus in their key to the New Zealand Chironomidae; *C. zealandicus*, *C. analis* (which possess 2 pairs of anal gills (ventral tubules, **Fig. 2.9**) and *C.* sp. a. (ventral tubules absent). Martin and Forsyth (un-published data) have identified nine distinct New Zealand *Chironomus* karyotypes (**Table 2.2**). Martin provides a preliminary key for these nine species on the website: http://www.genetics.unimelb.edu.au/martin2/NZchirfile

Martin and Forsyth, have identified features for some of the species that appear to be distinctive (**Table 2.2**) (un-published data available on the website). 20 live specimens collected from the surface sediments of the gravity cores and the littoral zone from 10 lakes from the training set in this study were examined in an attempt to link sub-fossil head-capsules to each of the nine species, and to test the key provided by Martin and Forsyth. At this stage I am not confident that the mandible, mentum, and central teeth types (**Fig. 2.10**, **2.13**, and **2.14**) are reliable features for identifying the nine karyotypes identified by Martin and Forsyth, especially since information is not available for some of the types (**Table 2.2**).

To my knowledge Martin and Forsyth have not examined large numbers (>10) of specimens belonging to each karyotype to investigate intra-specific variation. Webb and Scholl (1985) found a great deal of intra-specific variation of these features when they examined at least 12 specimens from each cytologically distinct species of *Chironomus* from Europe. Conversely, there was little intraspecific variation of such characters as the presence/absence of ventral tubules, the character of the anal tubules (**Fig. 2.9**) and the nature of the gular pigmentation (**Fig. 2.11**). Webb et al. (1985) found that there was a small amount of intraspecific variation in terms of the number of striae on the ventromental plate (Vmp) (**Fig. 2.12**), and that the 26 taxa they

examined fell into two distinct groups. 23 taxa had less than 70 striae on the Vmp, while three taxa had greater than 70 striae.

It seems likely that only the gular pigmentation and the striae on the Vmp would be useful features for identifying New Zealand subfossil *Chironomus* head-capsules at this stage. The basal sections of the striae are preserved and very obvious in mounted sub-fossil and fossil material (**Fig. 2.12a** and **b**). More care would be required with regards to the gular pigmentation, as the pigmentation is sometimes lost in fossil material. The gular pigmentation may be a useful diagnostic feature for identifying Holocene *Chironomus* head-capsules however.

An examination of the head-capsules from the Lake Forsyth core (see **Chapter 3**) revealed that the pigmentation survived in this case for material that was up to ca. 7000 years old. The head-capsule depicted in **Fig. 2.11d** is probably ca. 2000 years old. Head-capsules with a large number (>60) of striae on the Vmp (**Fig. 2.12b**) and dark gular pigmentation (**Fig. 2.11d**) were identified as *Chironomus* sp. a in this study. *C*. sp. a was the only taxon with the larger number of striae on the Vmp (Martin and Forsyth unpublished data). No attempt has been made at this stage to subdivide the *Chironomus* headcapsules with < 60 striae on the Vmp in this study. The eight species with < 60 striae on the Vmp have been called *Chironomus* spp.

Table 2.2 and **Fig. 2.9-2.14** (next page)

Table 2.2: provides a list of the nine *Chironomus* karyotypes identified by Martin and Forsyth (unpublished data). A list of the names given to each karyotpye is provided in the first column. The subsequent columns refer to diagnostic features identified by Martin and Forsyth. Transmission microscope images and scanning electron microscope (SEM) images are provided to illustrate the variation present in the genus *Chironomus* with respect to each of these morphological features.

Fig. 2.9: Posterior segments of the larval body showing the variation in the anal tubules (At) and the presence or Absence of the ventral tubules (Vt). Location of the procercus (P) is indicated. **a)** Rainbow Ski-field: long anal tubules, ventral tubules present; **b)** Horseshoe Lake: short pointed anal tubules, ventral tubules present; **c)** Lake Forsyth: very short pointed anal tubules, ventral tubules absent. Scale bar = 500 µm

Fig. 2.10: Variation in the pigmentation of the third accessory tooth of the mandible (from Webb and Scholl (1985). **a)** Type 1: light; **b)** Type 2: darker **c)** Type 3: completely dark. Scale bar = 50 µm.

Fig. 2.11: Variation in the pigmentation of the gular region on the head-capsule. **a)** Rainbow Ski field; **b)** Lake Evelyn; **c)** Horseshoe Lake; **d)** Lake Forsyth. Scalebar = 500 µm.

Fig. 2.12: Variation in the number of striations on the ventromental plate. Both specimens are sub-fossil material. the base of the striations are clearly visible (informally referred to as the "lashes'). **a)** Princess Bath; **b)** St Anne's Lagoon. Scalebar = 25 µm.

Fig. 2.13: Three main mentum types (from Webb and Scholl (1985)). **a-c)** Type I: laterals 3-6 in line; **d-e)** Type II: laterals 5 and 6 of equal height, 4th lateral taller than in type I so that a line connecting laterals 4 and 6 does not contact with the top of lateral number 5; **g-i)** Type III: lateral 5 much smaller than 6. Scale-bar = 25 µm.

Fig. 2.14: Four types of central tooth arrangement (from Webb and Scholl (1985)). **a & b)** Type I: C1 and C2 teeth joined, C1 broad, C2 asymmetrical; **c & d)** Type II: C1 and C2 separate, C1 broad, C2 symmetrical; **e & f)** Type III C1 and C2 separate, C1 narrow, C2 asymmetrical; **g & h)** Type IV: C1 and C2 separate, C1 narrow and short, C2 symmetrical. Scalebar = 25 µm.

Table 2.2: Information from Martin and Forsyth (unpublished): http://www.genetics.unimelb.edu.au/martin2/NZchirfile

Karyotype	LENGTH (mm)	VENTRAL TUBULES	MANDIBLE	MENTUM	C1 TOOTH	VMP STRIATIONS	ANAL TUBULES	GULAR REGION
C. species a	15.3-21.5	-				> 60	Short, pointed	Most very dark
C. forsythi	12.2-20	-				< 60	Long, constriction near middle	Posterior third
C. sp. 9	13-15	-				< 60	Short, pointed	Dark
C. sp. 6		-	I -> 2	II, last laterals turned out	Broad	< 60	Short, pointed	All Dark
C. analis	15.3-19	-	2	III, C2 teeth well seperated (II)	Narrower	< 60	Short, pointed	Most very dark
C. 'thermarum'	~11.3	+	2	II, C2 teeth partly seperated (I)	Narrower	< 60	Short, pointed	Darkened
C. sp. 8	18-19	+				< 60	Long and rounded	Some darkening posterior gula
C. novae-zealandiae	10-20	+	2	II, C2 teeth partly seperated (I)	Broad	< 60	Short, pointed	Very Dark
C. sp. 7	16-19	+				< 60	Short, pointed	Darkened

Fig. 2.9: Anal & Ventral tubules

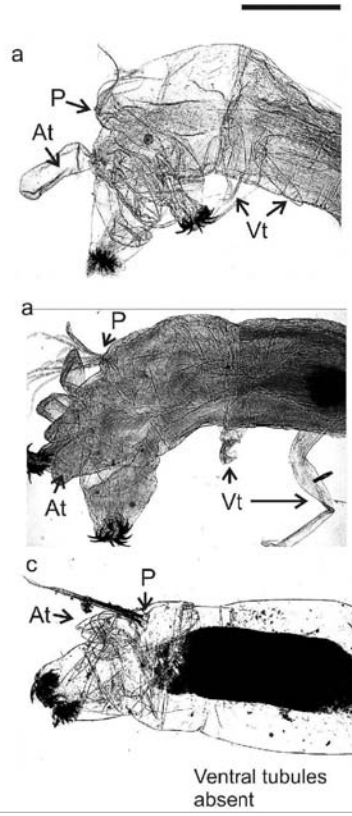


Fig. 2.10: Mandible type

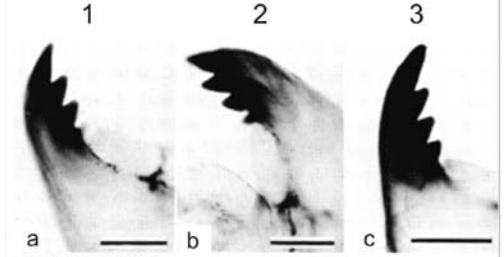


Fig. 2.11: Gular pigmentation

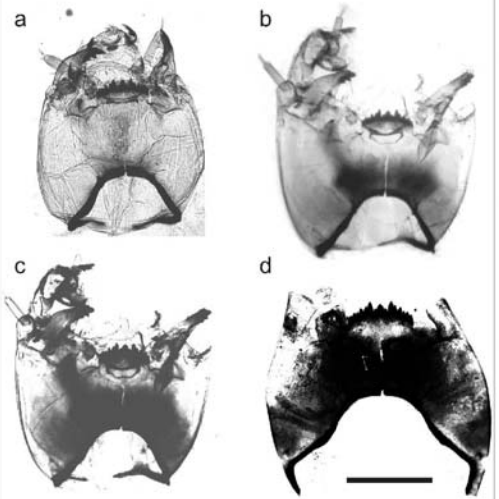


Fig. 2.12: Ventromental plates

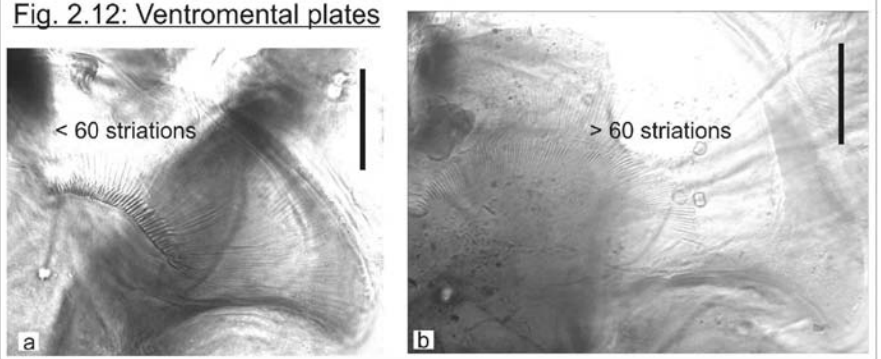


Fig. 2.13: Mentum type

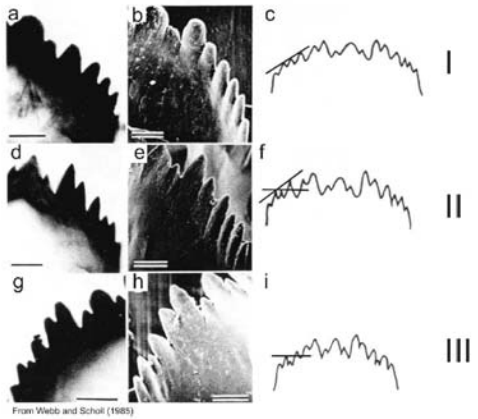
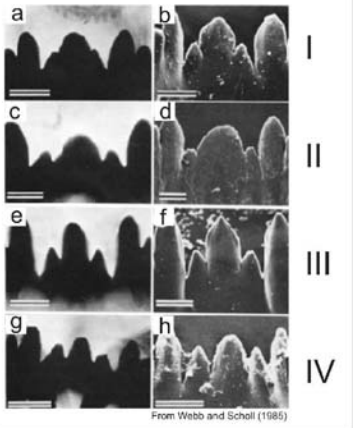


Fig. 2.14: Central tooth



It was observed however that the head-capsules from *Chironomus* larvae present in the high altitude (>1600m) micro-oligotrophic lakes had long rounded anal tubules, ventral tubules (2.9a) and very light pigmentation of the gular region (**Fig. 2.11a**). These characteristics are typical of *Chironomus* sp. 8 as identified by Martin and Forsyth (unpublished data) (**Table 2.2**).

2.4 ORTHOCLADIINAE

A total of 26 taxa including 10 undescribed species were encountered in the surface sediments during the course of this study. Most of these are easily identified based on the character of the mentum (number of teeth and shape) the shape of the head-capsule, and the presence or absence of a ventromental 'loop' and /or beard (**Fig. 10a** and **52a**, **Appendix A**). The identification of 21 of the Orthocladiinae taxa was based on publications by Boothroyd and Cranston (1994); Boothroyd (2002) and a preliminary key to the Orthocladiinae larvae of New Zealand (Boothroyd, unpublished).

Of these 21 taxa the species belonging to the genus *Cricotopus* and *Paratrichocladius* (Fig. 37-40, Appendix B) can be the most difficult to differentiate, especially if the mandibles are missing in the fossil material. *Cricotopus aucklandensis* (**Fig. 37**, **Appendix A**) is usually the easiest to identify based on the relative sizes of the central tooth and the 1st laterals. Differentiating *Paratrichocladius pluriserialis* from *Cricotopus zealandicus* is more difficult; both have 1st laterals that are ca. 0.5X the width of the central tooth. Boothroyd (2002) separates these species based on the presence of spines on the inner margin of the mandible (*C. zealandicus*) and the presence of a rugose margin on the outer margin of the mandible in the case of *P. pluriserialis* (**Fig.38b** and **39b**, **Appendix B**). Boothroyd (2002) also notes that the mentum of *P. pluriserialis* tends to be uniformly darkened (**Fig.38a**, **Appendix A**). Although he does not mention it in the, key the central four teeth tend to be lighter than the outer eight for *C. zealandicus* (**Fig. 39a**, **Appendix A**). The 2nd lateral is also much smaller relative to the 1st and laterals 3-6 are tightly clustered and more asymmetrical on the mentum of *C. zealandicus* (**Fig. 39a**, **Appendix A**).

I also collected 7 previously unreported and undescribed Orthocladiinae morphotypes were encountered during this study. I have informally named these Orthoclad sp. E, G, I, J and 1/6 for the sake of continuity with the undescribed Orthocladiinae taxa recorded by Boothroyd (unpublished) and unpublished subfossil chironomid descriptions of Vandergoes. A brief description and figures depicting the diagnostic features for each of these taxa is provided in **Appendix A**. The head-capsule belonging to Orthoclad species 1/6 was the best preserved out of these undescribed taxa and therefore allowed a more complete description and depiction of the

more diagnostic features (**Fig. 35a-e** and **36** in **Appendix A**). All references to figures in the description refer to **Appendix A**

*Head capsule small, ca. 100 µm in length from the tip of the central tooth of the mentum to the base of the thick darkly pigmented postocciptial border (**Fig. 36**). Dark pigmentation except for lighter areas around the ocelli. Mentum with broad central tooth rounded and converging to a small sharp peak. Six laterals. Laterals appear darker than the central tooth because of the presence of ventromental plates behind these teeth. Submental setae directly below the posterior termination of the ventromental plate, i.e. directly below the mentum (**Fig. 35b**). Prementum appears to be composed of numerous rows of small scales (similar to the Podonominae) Mandible with short apical tooth and six accessory teeth. Second inner tooth shorter than first and second inner teeth. Fifth and sixth inner teeth very small. Broad mandibular brush towards the base of the mandible. Three distinctive setae in the bottom half of the mandible, one close to the outer margin at the point of maximum curvature, and two clustered closely together directly opposite the base of the mandibular brush. Large spine extending directly towards the tip of the basal teeth from the molar region (**Fig. 36e**). Pre-mandible simple and bifid (**Fig. 36d**). Antennae with five segments, antennal blade stunted, being approximately the same length as antennal segment number 3 (**Fig. 36c**).*

The general appearance of the mentum is similar to *Smittia* (**Fig. 33**, **Appendix A**), but the mandible is quite different, with 6 inner teeth, lacking a seta subdentalis and with a broad mandibular comb near the base. The mentum of Orthoclad species 1/6 closely resembles *Krenosmittia* from the northern hemisphere (Cranston et al., 1983) which also has 6 laterals on the mentum, and a bifid premandible. The presence of a thick post-occipital border is reminiscent of the Diamesinae (e.g. *Maoridiamesa*, **Fig. 28**, **Appendix A**), while the presence of a prementum comprising small scales is reminiscent of the Podonominae (e.g. *Parochlus*, **Fig. 54**, **Appendix A**).

2.5 PODONOMINAE

The Podonominae are represented in the chironomid training set by three genera; *Podonomus*, *Parochlus* and one head-capsule tentatively assigned to *Podochlus*. 10 species of adult *Parochlus* have been described from New Zealand (Brundin 1966) but it is not possible to differentiate the larval forms at this stage. Stark and Winterbourn (2000) describe the larvae from *Parochlus* as having a middle tooth on the mentum that is considerably broader and longer than the laterals. Upon closer inspection the central tooth is actually trifid, comprising one central tooth and two

smaller first laterals (**Fig. 54**, **Appendix A**). Stark and Winterbourn (2000) distinguish the larvae of *Podonomus* from *Parochlus* by the presence of a small central tooth that is not much broader or longer than the 7-8 laterals (**Fig. 55 a**). The mandibles of these genera are also useful when they are present, especially since the central teeth of the mentum are sometimes difficult to differentiate when worn. *Parochlus* typically has 7 teeth on the mandible with the first inner tooth much larger than the rest (**Fig. 54**, **Appendix A**). *Podochlus* also has 7 teeth on the mandible, but the first inner tooth is about the same size as the apical tooth (**Fig. 55b**, **Appendix A**).

2.6 DIAMESINAE

Stark and Winterbourn (2000) mention three genera belonging to this sub-family; *Lobodiamesa* (1 species), *Maoridiamesa* (5 species) and larvae resembling the South American genus *Limaya*. Only head-capsules belonging to the genus *Maoridiamesa* were found in the 46 lake training set. It is not possible to distinguish between the four species known from adults and pupae that inhabit the New Zealand mainland (Stark and Winterbourn 2000). Therefore all head-capsules with a large black collar, three broad central teeth and 5 laterals and premental brushes (when preserved) (**Fig. 28**, **Appendix A**) were referred to as *Maoridiamesa*.

CHAPTER 3: A HOLOCENE RECORD OF HUMAN INDUCED AND NATURAL ENVIRONMENTAL CHANGE FROM LAKE FORSYTH (TE WAIREWA)

3.1 INTRODUCTION

This chapter presents the results from a multiproxy study of a record from Lake Forsyth (Te Wairewa), Banks Peninsula, Canterbury, New Zealand (**Fig. 3.1**). This study was conducted before the development of the chironomid-based transfer-functions (**Chapters 4-6**) and therefore served as a pilot study investigating the potential of the New Zealand Chironomidae as biological proxies in coastal brackish lakes. All of the previous chironomid-based paleoecological studies in New Zealand (Deevy, 1955; Boubee, 1983; Schakau, 1986; 1991; 1993) have focused on inland freshwater lakes. Many of New Zealand's shallow coastal brackish lakes and lagoons (including Lake Forsyth) are highly productive (eutrophic-hypertrophic[1]) (Jeppesen et al., 2000; Schallenberg and Burns, 2003; Woodward and Shulmeister, 2006; Canterbury Regional Council unpublished monitoring data). Although there have been some short-term (< 10 years duration) studies investigating the role of externally- driven physical factors (e.g. wind re-suspension of sediments, salt water incursions) on the biology and water chemistry of such lakes (e.g. Schallenberg and Burns, 2003). There have been no paleolimnogical studies that have provided detailed information on the influence of human disturbance (e.g. agriculture, deforestation) on the chemistry and biology of New Zealand's coastal lakes. Harvey (1996) conducted a diatom-based paleoecological study of Lake Ellesmere (Te Waihora) (**Fig. 3.1**), but the focus of this study was on salinity changes resulting from the opening and closing of the Kaitoreti 'Spit'.

There is historical literature referring to Lake Forsyth and its catchment extending back to the late 1830s (Petrie, 1963; Soons, 1998), while lake monitoring data consists of an almost continuous record from 1993 (Canterbury Regional Council, unpublished data). This historical data and information from other environmental proxies provided a source of comparison for the chironomid data. Fossil pollen (and radiocarbon dating) was used to tie the lake record to known history of deforestation and subsequent pastoral farming in the catchment (Petrie, 1963).

1. All trophic classifications are based on trophic level index (TLI) classification system of Burns et al. (2000)

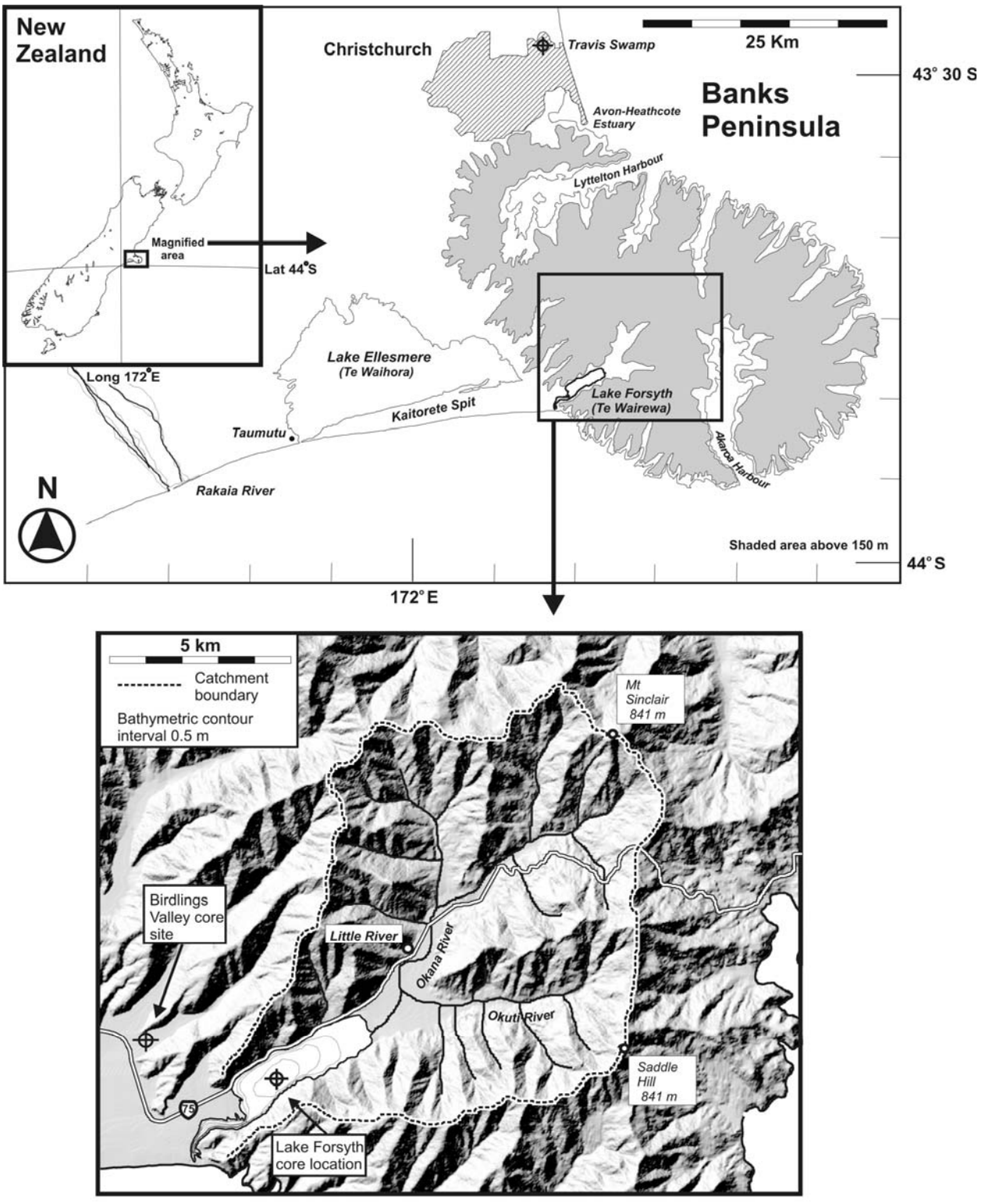


Fig. 3.1: The location of Lake Forsyth (Te Wairewa), the lake bathymetry (contours = 40cm water depth), and the catchment boundary. The location of two other sites mentioned in the text (Birdlings Valley and Travis Swamp) are also shown.

There has been a great deal of research investigating the ecology of the New Zealand foraminifera (e.g. Hayward et. al., 1996). Foraminifera found at the base of the Lake Forsyth core provided information on changing salinity in the lake in the past. This project was a collaborative project with Michael Reid from NIWA (National Institute for Water and Atmospheric research). A diatom based transfer-function for salinity (Reid, 2005) was also applied to this core which will provide a further point of reference for the chironomid data when the results are available.

This study was also intended to provide a long-term record of environmental change from Lake Forsyth to provide guidance for the future management of this water body. Many restoration based paleolimnological studies assume slow or no natural change in the aquatic ecosystem being examined. In the case of Lake Forsyth, however, recent environmental changes are the result of both rapid coastal evolution (a 'natural' phenomenon) and human disturbance. This chapter provides a case study in the use of a multiproxy paleobiological approach to distinguish between human impacts and the development of a near coastal waterway system.

This investigation involves the first use of Trichoptera (caddisflies) as a paleoenvironmental proxy in New Zealand. While chironomids have now been used extensively in the Northern Hemisphere (e.g. Brooks et al., 1997; Quinlan and Smol, 2002; Brooks and Birks, 2004) Trichoptera have only been used in a few paleoenvironmental studies (e.g., Ponel et al., 1999; Solem and Birks, 2000; Greenwood et al., 2003). The larvae of modern Trichoptera species are common in many lentic and lotic habitats (Greenwood et al., 2003). Like the Chironomidae, information on the ecology and distribution of modern Trichoptera larvae can be used to derive paleoenvironmental information from fossil species. Trichoptera larvae are usually represented by the chitinous sclerites, mandibles (**Fig. 3.5b**), appendages (**Fig. 3.5c**) and the remains of cases constructed from sand grains or organic detritus (**Fig. 3.5a**). In this study the Trichoptera are represented by a single species, *Oecetis unicolor* McLachlan. However, the ecology and distribution of this species is well documented (e.g. Stark, 1981; Timms, 1982; 1983) and even the addition of this one species provides useful information.

3.1.1 Location and site information

Lake Forsyth (Te Wairewa) (43° 48 S, 172° 44 E) is a shallow (< 4 m deep), hypertrophic, slightly brackish lake situated on the southern side of Banks Peninsula, on the east coast of the South Island, New Zealand (**Fig. 3.1**). The lake is isolated from the Pacific Ocean by a narrow (≤ 100 m) gravel barrier that is an extension of the Kaitorete "Spit". Kaitorete "Spit" extends some

30 km from Taumutu in the south to the flanks of Banks Peninsula in the north.

The present configuration of Kaitorete "Spit" (more accurately described as a relict spit and active barrier beach complex) has evolved over a period of ~ 8000 years as a result of the accumulation of material transported north along the Canterbury Bight by long shore currents (Soons et al., 1997). Historical accounts state that cargo vessels navigated the channel connecting Lake Forsyth to the ocean until the late 1830s, however it was possible to walk across the barrier by 1843 (Soons, 1998). The lake normally drains by percolating through the gravels of the barrier. However, the lake is artificially opened when lake levels are high to prevent the flooding of local roads and farms. The gravel barrier was first artificially opened in 1866, and is currently opened about once every year, depending on rainfall (Main, 2002).

The lake catchment covers approximately 110 km^2 ranging from about sea level to 840 m (amsl) (**Fig. 3.1**). Most of the catchment was covered in broadleaf/podocarp forest until ~ 1895, by which time most of the trees had been removed for timber, or burnt in fires (Petrie, 1963).

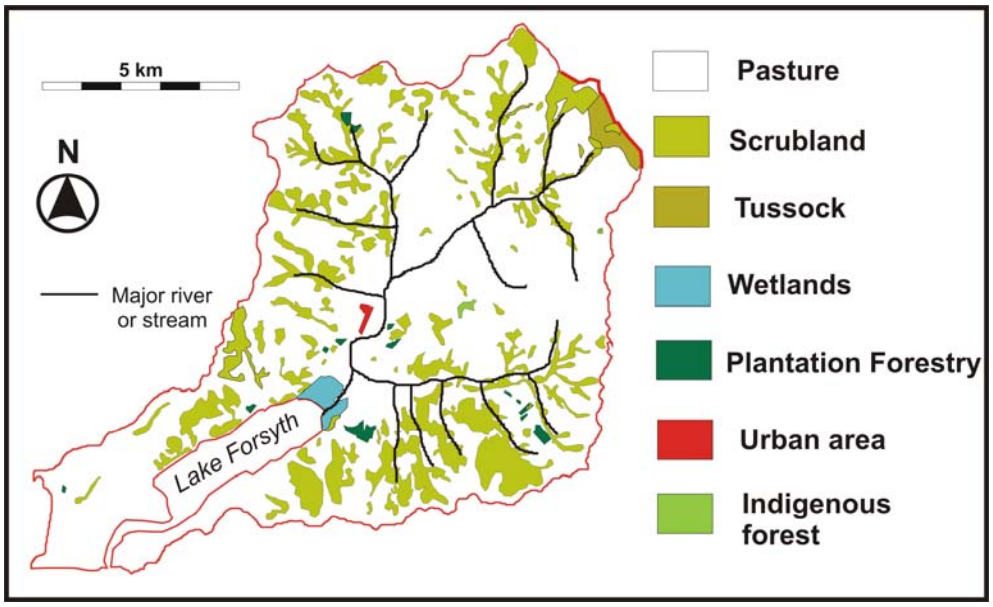


Fig. 3.2: Present land-use and vegetation cover in the Lake Forsyth catchment.

Since deforestation, most of the catchment has been used for pastoral agriculture and only small patches of the original forest cover remain (**Fig. 3.2**). After 1907 the lake became prone to regular blooms of the hepatotoxic cyanobacteria *Nodularia spumigena* Mertens, which have been associated with the appearance of large numbers of dead fish (Main, 2002). There is currently a significant long-fin eel (*Anguilla dieffenbachia* Gray), population in the lake, but Maori oral tradition recalls a more diverse and abundant fish fauna in the past (Main, 2002).

3.2 MATERIAL AND METHODS

3.2.1 Coring

A percussion corer was used to obtain a 1.2 m sediment core (FORS1- LC) from the deepest point of the main depositional basin (**Fig. 3.1**). The top 10 cm of this core collapsed due to a high water content. A short (50 cm) gravity core was recovered from the same location to allow sampling of this part of the sequence. The sharp transition from light grey gyttja to dark green aqueous material at ~ 10 cm (**Figs 3.4** and **3.6**) was the basis for correlation between these two cores.

The main core was divided into two sections. One half was archived in a cool store, while the remaining half was sub-sampled at 1 cm intervals. The gravity core was extruded and sub-sampled on site at 1 cm intervals. The sub-samples were bagged and stored for subsequent processing for palynomorphs and macroinvertebrates.

3.2.2 Chronology

A single sample was recovered at 108-110 cm for AMS radiocarbon dating. The sample comprised organic lake mud, which was dried in an oven for three days at 57 °C, ground and homogenized. 5 grams of the resulting powder was sent to the Rafter Radiocarbon Laboratory, Lower Hutt, New Zealand for AMS dating.

3.2.3 Pollen and charcoal analysis

Pollen slides were prepared for analysis following the standard methods outlined in Moore et al. (1991). Two *Lycopodium* tablets (Department of Quaternary Geology, Lund University, Sweden. Batch no. 124961) were added to each sample to facilitate the calculation of pollen concentrations (Stockmar, 1971). Palynomorphs were identified and counted under a transmitting light microscope with the aid of publications by Pocknall (1981), Large and Braggins (1991), Moore et al. (1991), and Moar (1993). Podocarp pollen was frequently encountered in the form of damaged grains consisting of a corpus with only one sacchus attached, or as an individual sacchi or corpi. In these cases the grains were counted as half grains. The pollen slides were also analysed for charcoal content using the Clark (1982) point count estimation method.

3.2.4 Invertebrate paleontology

Sediment samples were processed for invertebrates following a modified version of the chironomid processing method outlined in Walker (2001). It was discovered that this method was also successful in extracting the remains of Trichoptera (caddisfly larvae and cases), molluscs, and foraminifera from this core. Samples were deflocculated in hot 10% KOH and washed through a 93 μm mesh with copious amounts of distilled water. Initial trials with samples from this locality revealed that a quantity of sediment remained inside chironomid head-capsules, obscuring much of the detail required for identification. This problem was resolved by heating the resulting sediment residue in a 10% solution of Calgon ®. Samples were then transferred to a Bogorov counting tray and examined for invertebrate remains under a dissection microscope, at 50x magnification.

A preliminary examination of sediment samples from the FORS1-LC core revealed a low chironomid species diversity. Heiri and Lotter (2001) and Quinlan and Smol (2001), have shown that a sample size of 45-50 head capsules is a representative sample of chironomid communities where diversity is low. Sufficient sediment was processed in order to obtain this minimum head capsule abundance. An average of 10 ml of wet sediment was required to achieve the target head capsule quantity. A corresponding 2 ml sample from each horizon was dried at 50 °C for 3 days and weighed, to enable the calculation of head-capsule concentration per dry weight of sediment.

Insect remains (chironomids, Trichoptera, etc.) were mounted on glass slides in a drop of polyvinyl lactophenol and covered with a glass coverslip. Chironomid head capsules were mounted ventral side up to facilitate identification. Trichoptera larval cases were transferred to a vial of ethanol for preservation to prevent distortion by slide mounting. Foraminifera were mounted on cardboard slides using a tragacanth gum.

Chironomids and Trichoptera were identified using a transmission light microscope with the aid of publications by Forsyth (1971), Boubee (1983), Shakau (1993) and Winterbourn et al. (2000). Foraminifera were identified under a dissecting microscope with the aid of Hayward (1999).

3.2.5 Numerical analysis and display of data

Zonation of pollen and aquatic faunal stratigraphy

The results of the pollen analysis and invertebrate paleontology were plotted using Psimpoll 3.10 (Bennett, 2002). Pollen data were displayed as percentage data with a corresponding pollen concentration (**Fig. 3.4**), while the abundance of chironomids, forams, caddis cases and *Pediastrum simplex* Meyen colonies were plotted as concentrations per gram of dry sediment (**Fig. 3.6**).

The Shannon Weaver Index (H') was used as a measure of the diversity of the aquatic faunal species assemblage. H' was calculated using the equation: $H' = - \sum P_i \ln P_i$, where P_i represents the proportion of the *i*th taxon in the sample (Begon et al., 1986). Calculations were based on the concentrations (per gram of dry sediment) of chironomids, trichoptera, and foraminifera present in each sample. The resulting curve of diversity with respect to depth is included in **Fig. 3.6**.

The CONISS function in Zone 1.2 (Juggins, 1992) was used to determine the location of the zone boundaries. The analysis was based on the percentage and concentration data standardized to a mean of zero and to unit standard deviation (Grimm, 1987). Separate zone analyses were run on pollen percentage data and concentration data for the aquatic fauna (chironomids, forams, trichoptera, and *P. simplex*) so that zonation in each record distinguished between changes in catchment vegetation and changes in lake taxa.

Podocarp pollen found between 55 and 90 cm was poorly preserved and consequently a large proportion was classified as undifferentiated podocarp pollen (**Fig. 3.4**). This zone of poor preservation was identified as a zone by the zone analysis. The percentage data for the podocarp pollen was combined for the sake of the zone analysis, to remove the effect of the preservation bias.

Exploratory analysis of aquatic faunal stratigraphy

Exploratory data analysis of the concentration data for the aquatic taxa was performed using CANOCO 4.5 and displayed using Canodraw (ter Braak and Šmilauer, 2002). Stratigraphic trends in the species concentration data were investigated using principal components analysis (PCA), as an initial detrended correspondence analysis (DCA) of the log-transformed data revealed that gradient lengths were less than 2 standard deviations (Jongman et al., 1987). The PCA ordination was performed on centered and standardized species data with a focus on inter-sample distances, to reduce the effects of taxa with high concentrations (e.g., *P. simplex*). The samples were connected

as a time-track to show the changes in species composition with respect to stratigraphic depth.

Determining the relationship between regional vegetation and aquatic fauna

Redundancy analysis (RDA) was used to explore the relationship between aquatic taxa and regional vegetation. The RDA was performed in CANOCO 4.5 (ter Braak and Šmilauer, 2002) using aquatic taxa concentrations (units g^{-1} of dry sediment) for the species data and pollen percentages as environmental data. Pollen percentages for each taxon were assigned to the 6 main vegetation classes listed in the regional vegetation summary in **Figs 3.4 and 3.6** (Podocarp/Broadleaf Canopy Trees, Podocarp/Broadleaf Secondary Trees, Low Forest and Scrub, Herbs and Grass, Native Disturbance Indicators, and Exotic Trees). Pollen percentages for all taxa belonging to a particular class were combined to give 6 totals, one for each pollen class. It was assumed that the use of combined pollen percentages would provide a clearer indication of regional vegetation trends and reduce the effect of the many species in the record that were present in low concentrations. Examples of the main species belonging to each class are depicted in **Fig. 3.4**, except for Podocarp/Broadleaf Secondary trees. Abundance curves for pollen from these smaller trees and shrubs that are typical of podocarp/broadleaf forest (e.g. *Shefflera digitata* Forster, *Pittosporum* spp. Hook and *Myrsine* spp. Linnaeus) were omitted from the summary diagram for the sake of clarity, as none of the individual species abundances exceded 5%. Raw counts for all of the taxa identified can be found in **Spreadsheet E2** on the supplemetary data disc (**Appendix E**).

The redundancy analysis was performed on abundance data taken from above the disappearance of the last salt-tolerant foram species from the record (*Ammonia parkinsonia f. aoteana* Finlay) at about 90 cm depth. This change in aquatic species composition was accompanied by changes in sedimentology, but there was a lack of any major corresponding signal in the pollen record (**Figs 3.4 and 3.6**). It was therefore assumed that these changes in the aquatic fauna were the result of the formation of a barrier isolating the Lake Forsyth Basin from the ocean, not changes in regional vegetation. Consequently data for the basal 30 cm of the core was omitted from the analysis to avoid interference with the vegetation/aquatic species correlation. The aquatic invertebrate record was based on a higher sample resolution than the pollen stratigraphy. In performing the numerical analysis, samples from the invertebrate record were only used if they had stratigraphic equivalents in the pollen record.

3.3 Results

3.3.1 Stratigraphy and chronology

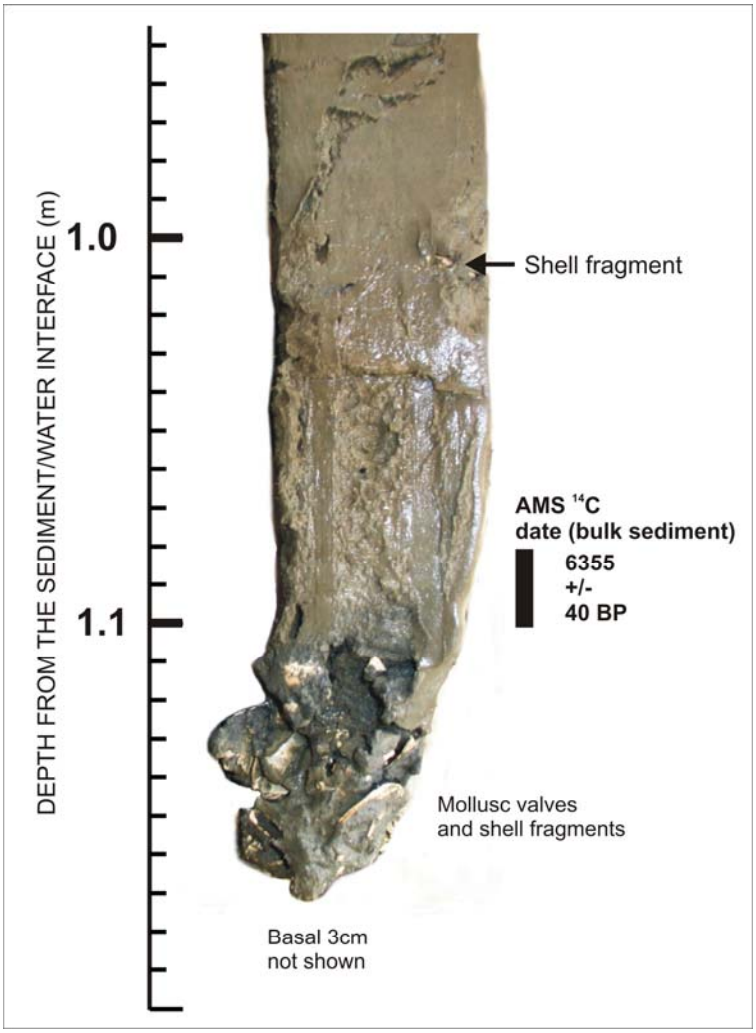


Fig 3.3: Photograph of the basal 22cm of the core (FORS1-LC) showing the transition from a matrix supported shell 'hash' at the base to a silty lake mud at about 1.1 m depth. Note the presence of a shell fragment at about 1m depth (indicated by an arrow). The basal 3cm of the core is not shown in this image but is exactly the same as the dark grey sandy unit that extends to ca. 1.1m depth. The basal section of the core remained in the basal collar of the core chamber after extrusion of the core and was therefore stored separately.

The 1.2 m sediment core (FORS1-LC) was divided into six units (**Figs 3.4** and **3.6**) using the Troels-Smith system (Troels-Smith, 1955). The basal 10 cm consisted of a dark grey sandy unit containing abundant large (≤ 2 cm) shell fragments, valves, and one set of attached valves, mainly from *Chione (Austrovenus) stutchburyi* Wood (**Fig. 3.3**). The shell fragments were more concentrated in the top 6 cm of the sandy unit. This basal sandy unit was overlain by a 10 cm thick light brown sandy clay horizon; an AMS radiocarbon date from this horizon (108-110 cm) provided an uncalibrated date of 6355 +/- 40 BP (NZA 18809). This radiocarbon date was calibrated using INTCAL98 (Stuiver et al. 1998) and yielded an age range of 7331 to 7211 BP at 2 σ.

The proportion of sand gradually decreased to the top of the sandy clay horizon at 100 cm depth. The sandy clay horizon was overlain by ~ 35 cm of light brown silty clay. At 63 cm depth, a 30 cm

thick layer was differentiated on the basis of an increasing proportion of herb detritus. The top 30 cm of the core was characterized by a rapid increase in the clay content, with the sediment becoming more aqueous and organic rich. The top 10 cm consisted of a dark green aqueous layer which comprised highly humified organic matter.

3.3.2 Pollen and charcoal analysis

The pollen assemblage was dominated by spores from the tree fern *Cyathea* spp. Smith, which contributed up to 73% of the non-swamp pollen total (**Fig. 3.4**). *Cyathea* spp. spores were usually poorly preserved and showed signs of physical damage or chemical corrosion. The relative abundances for the remaining 150 species found in the record were expressed as percentages, based on the non-swamp (n. sw.) total, and non-swamp total minus tree fern spores (non-swamp/non-spore: n. sw./n. sp.). A summary diagram depicting the relative abundances of the main taxa (maximum abundance ≥ 5%) is presented in Fig. 3.4. The regional vegetation summary (**Figs 3.4 and 3.6**) is based on the percentage data for all of the 150 species. A table containing raw counts for all taxa is located on the supplementary data disc (**Appendix E)**.

It was assumed that the high fern spore count was indicative of a high fluvial contribution to the pollen assemblage, as many of the spores showed obvious signs of long distance transport. Tree ferns are a common component of riparian vegetation in New Zealand forests (Dawson and Lucas, 2000) and are likely to be over-represented in river borne pollen derived from a forested catchment. Therefore, in order to provide a more meaningful signal of the regional vegetation, percentages of the other non-spore palynomorphs were expressed as a fraction of the pollen total minus both the swamp elements (Cyperaceae, etc.) and fern spores.

The Zone analysis in Zone 1.2 (Juggins, 1992) resulted in division of the pollen record into 3 main zones (I, II, and III) and 2 sub- zones (Ia and IIIa) (**Figs 3.4** and **3.6**). The zone analysis separated the stratigraphic samples into 20 clusters, but 5 of these clusters possessed a between cluster dispersion that was significantly greater than the remaining 15 clusters. The three clusters with the largest total dispersion (21.8, 18.5, and 16.9) were selected as the main zone boundaries. The 2 sub- zones were based on clusters with total dispersion values of 15.6 and 12.7. The highest total dispersion value for the 15 discarded clusters was 10.4.

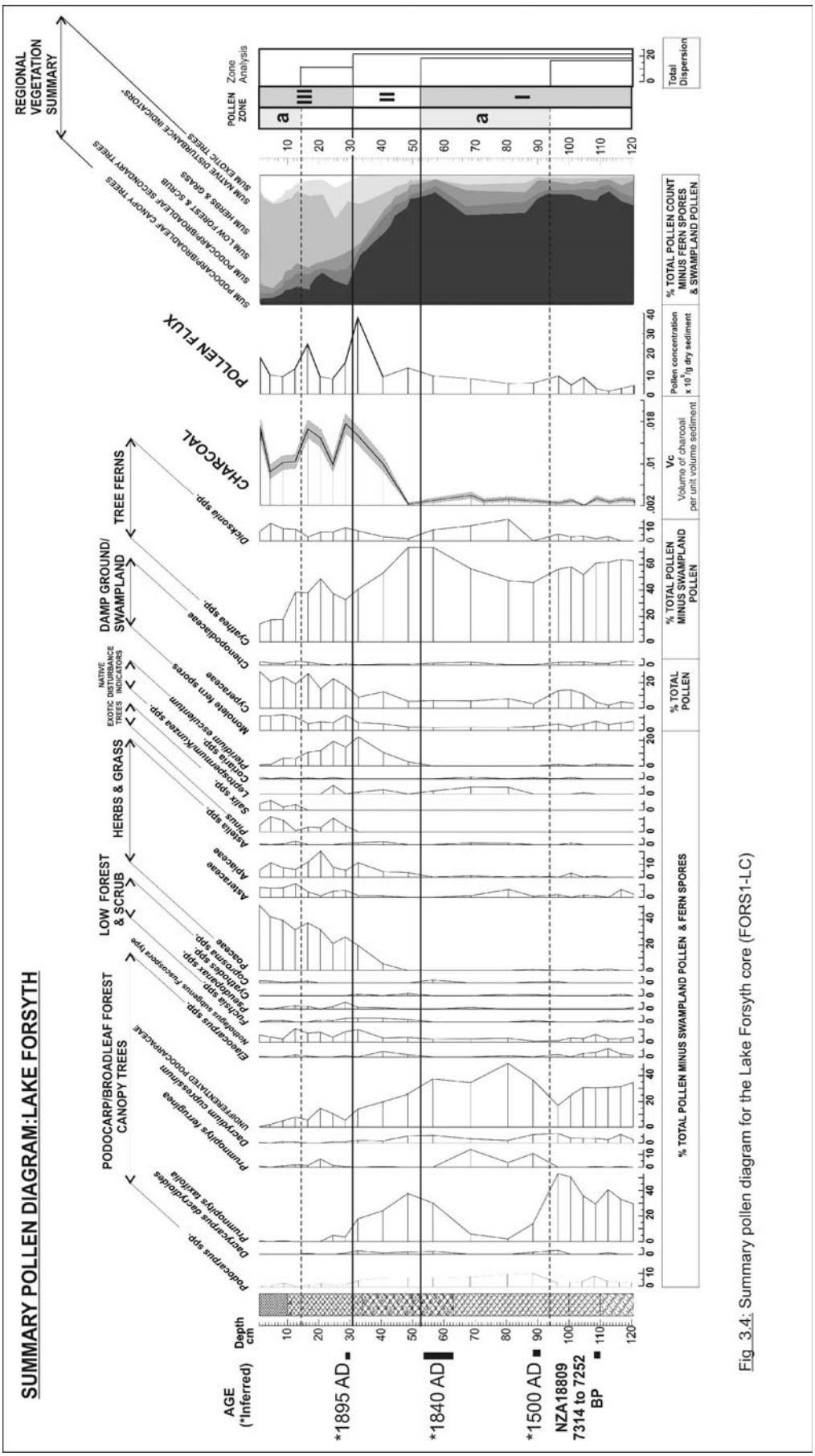


Fig 3.4: Summary pollen diagram for the Lake Forsyth core (FORS1-LC)

Zone I: 120 – 52 cm. Prumnopitys spp. and Podocarpus zone

Spores from *Cyathea* spp. dominate the n. sw. total, increasing from 60% to 70% at the top of this zone. The n. sw./n. sp. total is dominated by pollen from podocarp/broadleaf canopy trees; *Prumnopitys taxifolia* (≤50%), *Prumnopitys ferruginea* (≤10%), *Podocarpus* spp. (≤10%), and undifferentiated podocarp pollen types (≤50%). *Nothofagus* Fuscospora type is present at an average abundance of 5% of the n. sw./n. sp. total. There is a slight increase in the abundance of Cyperaceae pollen from 5% to 15% of the pollen total at about 100 cm depth.

Zone Ia: 94-52 cm. Leptospermum/Kunzea and Asteraceae zone

This zone is characterised by a decrease in the abundance of *P. taxifolia* from 50% to 5% of the n. sw./n. sp. total. There is also an increase in the abundance of *Leptospermum/Kunzea* spp. and Asteraceae pollen. This is accompanied by a minor increase in the proportion of pollen from *Coriaria* spp., *Astelia* spp., and pollen from various low forest and scrub taxa.

Zone II: 52 – 31 cm. Poaceae, Pteridium and Apiaceae zone

Cyathea spp. spores decrease in abundance from 70% to 40% of the n. sw. total at the top of this zone. This zone is also characterized by a decrease in the total contribution of podocarp/broadleaf canopy tree pollen from ~85% to ~20% of the n. sw./n. sp. total. This was accompanied by a peak in *Pteridium esculentum* at 33 cm, and an increase in the abundance of pollen from *N.* Fuscospora type; low forest and scrub, including *Pseudopanax* spp.; Apiaceae; Asteraceae and Poaceae, which increases from ~ 0 to 20 % of the n. sw./n. sp. total. There is also a rapid increase in the abundance of charcoal in the pollen samples.

Zone III: 30 - 0 cm. Poaceae, Pteridium, Pinus and Salix spp. *zone*

Pollen from two exotic trees; *Pinus* spp. and *Salix* spp., appears at 30 cm and 15 cm respectively. The steady decline of podocarp/broadleaf canopy tree pollen that began at 45 cm continues more gradually, with abundance decreasing from 20% to 10% of the n. sw./n. sp. total at the top of the core. Cyperaceae pollen increases from 15 % to ~ 30 % of the pollen total at the top of the core.

Zone IIIa: *14 – 0 cm Salix* spp. zone

This zone is characterised by the appearance of pollen from *Salix* spp. There is also a minor increase in Asteraceae pollen, while *Leptospermum/Kunzea* spp. pollen disappears from the record.

3.3.3 Invertebrate paleontology

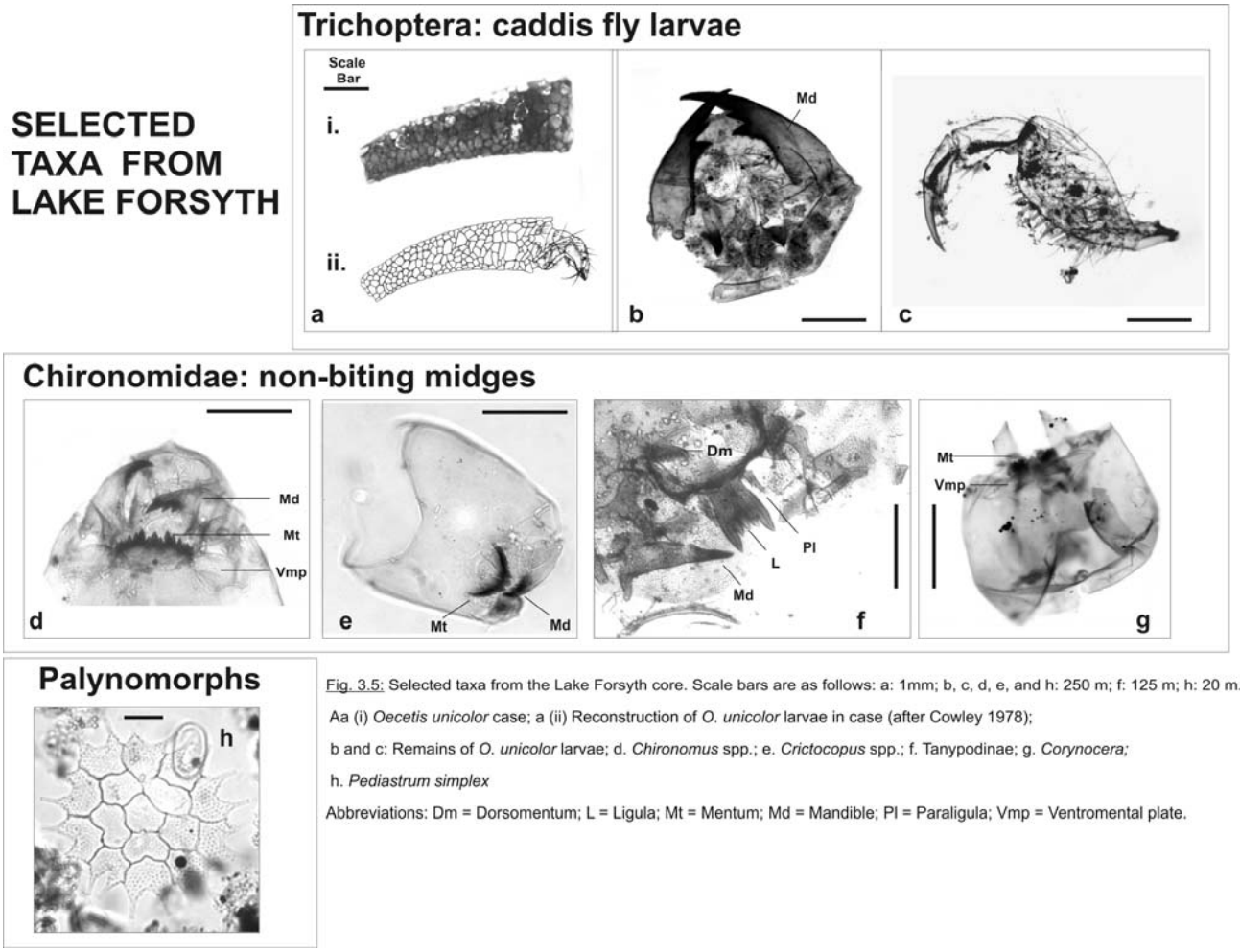


Fig. 3.5: Selected taxa from the Lake Forsyth core. Scale bars are as follows: a: 1mm; b, c, d, e, and h: 250 m; f: 125 m; h: 20 m.
Aa (i) *Oecetis unicolor* case; a (ii) Reconstruction of *O. unicolor* larvae in case (after Cowley 1978);
b and c: Remains of *O. unicolor* larvae; d. *Chironomus* spp.; e. *Crictocopus* spp.; f. Tanypodinae; g. *Corynocera;*
h. *Pediastrum simplex*
Abbreviations: Dm = Dorsomentum; L = Ligula; Mt = Mentum; Md = Mandible; Pl = Paraligula; Vmp = Ventromental plate.

Abundances of the main invertebrate taxa present in the Lake Forsyth core are presented in **Fig. 3.6**. The chironomid fauna was dominated by large numbers of head capsules that closely resemble *Chironomus zealandicus* Hudson, a species that was found living in the lake at the time of coring (**Fig. 3.5d**). At the time this pilot study was performed, it was only possible to identify the fossil head-capsules of this type to genus only, i.e. *Chironomus* spp.. However, recent work by Martin and Forsyth (unpublished) has identified nine *Chironomus* species on the New Zealand mainland (see **Chapter 2**). It is now possible to separate head-capsules from this genus into those with greater than 60 striations on the ventromental plate (*Chironomus* sp. a, **Fig 2.12b**) and those with less than 60 striations on the ventromental plate (all other *Chironomus* species, **Fig. 2.12a**). At this stage the slides from this core have not been re-counted in detail. A preliminary examination of all of the slides revealed that all head-capsules were from *Chironomus* sp. a which is probably synonymous with *Chironomus zealandicus* (Jon Martin pers. comm). I will continue to refer to the Chironomus

head-capsules as *Chironomus* spp. until a complete detailed re-count of the slides is performed.

The record was divided into five main zones (1-5), and two sub-zones (2a and 5a) selected from the 20 clusters produced by Zone 1.2 (Juggins, 1992) (**Fig. 3.6**). Zones were selected from the 20 cluster set on the basis of total dispersion values produced in the analysis. Dispersion values ranged from 40.1 (Zone 2/Zone 3 boundary) to 18.5 (Zone 2/Zone 2a boundary) (**Fig. 3.6**). Of the 13 rejected clusters the highest dispersion value was 12.9.

Zone 1: 120 – 106 cm. Chironomus spp. and foraminifera zone

This horizon yielded a chironomid head capsule concentration of 2.5 head capsules/g dry sediment, the lowest abundance for the entire core. The chironomid head capsules were derived exclusively from *Chironomus* spp. However there is a relatively diverse assemblage of benthic foraminifera (H'= 0.1 - 0.4). Three species of foraminifera were abundant in this section; *A. p. f. aoteana*, *Elphidium excavatum f. williamsoni* Haynes, and *Zeaflorilus parri* Cushman. *Z. parri* was sparse and only present at the base of the core, while the abundance of *A. p. f. aoteana* and *E. e. f. williamsoni* decreased up-section to the base of Zone 2. The remains of molluscs were abundant in Zone 1, with a conspicuous concentration in the upper 5 cm of the basal sandy unit. Most common were fragments and one set of attached valves belonging to bivalve *C. stutchburyi*. The gastropods *Potamopyrgus pupoides* Hutton and *Littorina* (*Austrolittorina*) *unifasciata* Philippi were also abundant.

Zone 2: 106 – 43 cm Chironomus spp. zone

Chironomid head capsules increased in abundance to ~10 head capsules/g of dry sediment. The chironomid fauna was still dominated by *Chironomus* spp., with the appearance of low abundances of *Cricotopus* spp. van der Wulp (**Fig. 3.5e**), *Corynocera* spp. Boothroyd (**Fig. 3.5g**), and *Tanytarsus vespertinus* Hutton. *A. p. f. aoteana* is present in low concentrations for the bottom ~15 cm of this zone. Upon disappearance of A. *p. f. aoteana* the overall diversity of the biological assemblage drops to 0 at the middle of this zone.

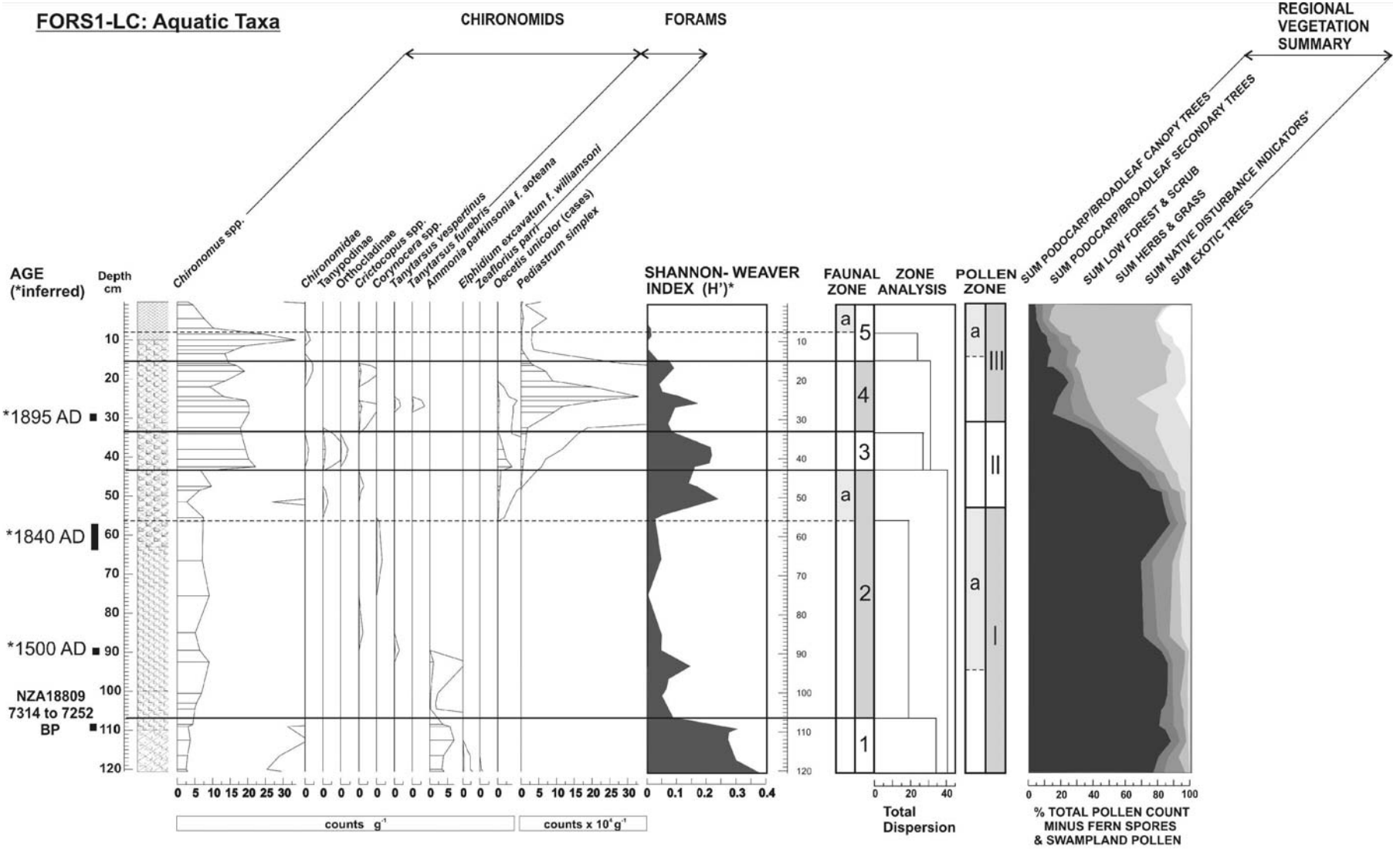


Fig. 3.6: Summary diagram of water quality proxies from the Lake Forsyth core. Pollen zones and a regional vegetation summary are provided for the sake of comparison.
*Shannon Weaver Index (H') = -Σ Pi ln Pi, where Pi represents the proportion of the i[th] taxon in the sample (Begon et al. 1986).

Zone 2a: 56-43 cm: Chironomus spp., Oecetis unicolor zone

The concentration of chironomid headcapsules remains constant while cases and remains from the caddisfly *Oecetis unicolor* (Figs 3a, b and c) are present in small concentrations. Headcapsules from the chironomid genus Tanypodinae (? *Gressittius antarcticus* Hudson) (Fig. 3.5f) are present for the first time in the record. Stellate cell colonies of *Pediastrum simplex* (Fig. 3.5h) appear for the first time in low concentrations at the top of this zone. Overall species diversity increases to 0.25.

Zone 3: 43-33 cm. Chironomus spp., Oecetis, Tanypod and Pediastrum zone

The concentration of chironomid head capsules increases from ~5 to ~20 head capsules/g dry sediment. *Chironomus* spp. still dominated while numbers of Tanypodinae head capsules increased. Larval cases from *O. unicolor* increased at ~ 42 cm yielding 4 cases g^{-1}dry sediment. The abundance of *P. simplex* colonies increases to ~2.5 colonies $x10^4$ g^{-1} dry sediment at the top of zone 3. Species diversity peaks at 0.25 at 40 cm then drops to 0.1 at the top of this zone.

Zone 4: 33-15 cm. Chironomus spp. and Pediastrum zone

Chironomid headcapsule abundance remained constant, except for a decline 50 and 55 cm. Tanypodinae head capsules disappeared from the record completely. Four chironomid species remain; *Chironomus* spp., *Tanytarsus funebris* Freeman, *T. vespertinus*, and *Cricotopus* spp. *Oecetis unicolor* cases and remains occurred in low concentrations before disappearing from the record completely at 20 cm. The concentration of *P. simplex* increases to a peak of about 30 colonies X 10^4 g^{-1} at 24 cm depth. *P. simplex* concentrations then return to the concentrations that were present in Zone 3. Species diversity remains approximately 0.1.

Zone 5: 15-0 cm: Chironomus spp. zone

Chironomus spp. headcapsules peak initially to the highest concentration for the entire core at 10cm. This peak is followed by a rapid decline to a low concentration of ~5 headcapsules g^{-1} dry sediment. Overall species diversity drops to 0, with *Chironomus* spp. remaining as the only faunal taxon at the top of the core.

Zone 5a: 8-0 cm. Chironomus spp. low concentration zone

Chironomus sp. headcapsules are present in low concentrations. Species diversity is low.

3.3.4 Numerical Analysis

PCA of aquatic species data

Figures **3.7a** and **b** present PCA plots of axes 1 and 2 of aquatic species and samples respectively, based on 13 aquatic species and 43 stratigraphic samples. A summary of the PCA statistics is presented in **Table 3.1**. PCA axis 1 (λ_1=0.285) contrasts salt-tolerant benthic foram species to the right of the diagram with high concentrations of *Chironomus* spp. and the freshwater algae *P. simplex* to the left. PCA axis 2 (λ_2 = 0.191) contrasts *O. unicolor*, Tanypodinae and Orthocladinae at the top, with *Cricotopus* spp. and *Tanytarsus* spp. at the bottom. Large distances between samples on the stratigraphic depth plot (**Fig. 3.7**) represent major changes in the aquatic fauna. There are two main phases of species composition change. The first major change in species composition occurs between 43.5 and 32.5 cm, which corresponds to faunal Zone 3 in **Fig. 3.6**. The second main period of species composition change occurs between 28.5 and 24.5 cm which occurs in the middle of faunal Zone 4 in **Fig. 3.6**.

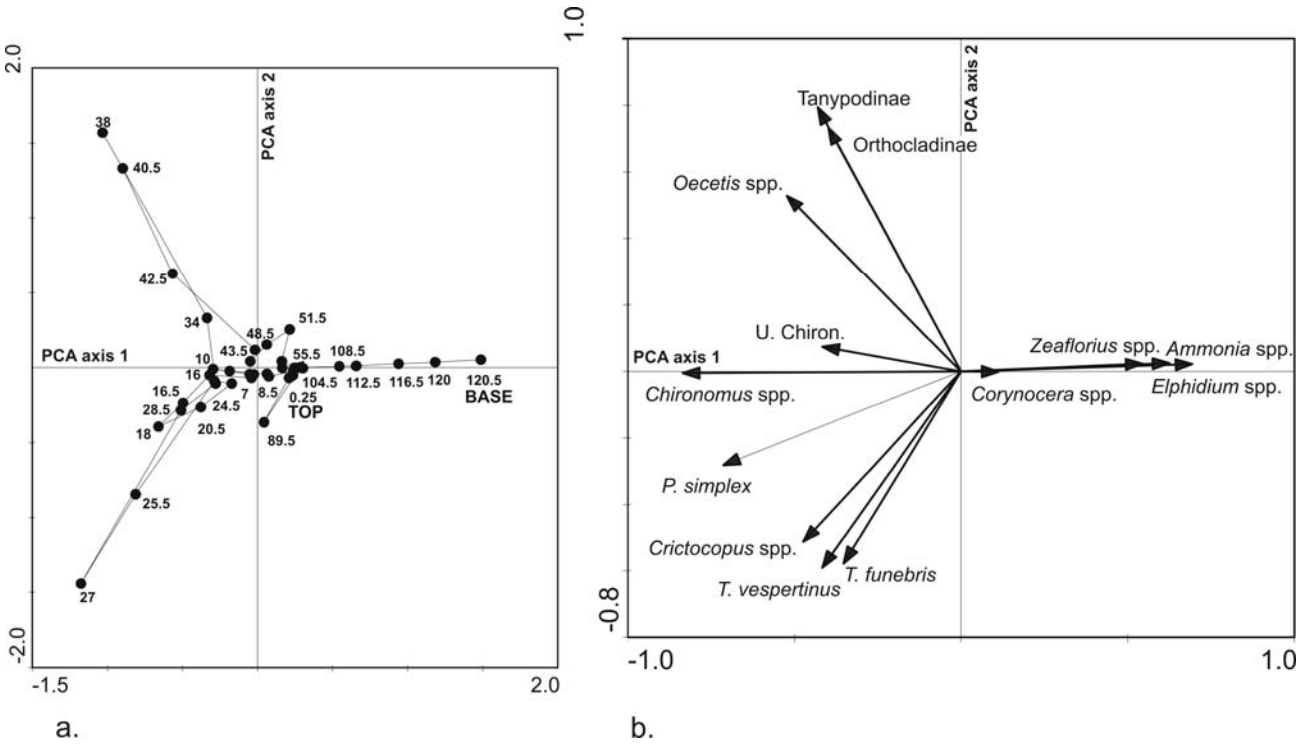


Fig. 3.7: PCA ordination plots of aquatic species and stratigraphic samples. a) Stratigraphic samples with depths labeled in cm from the top of the core. Fitted passively and connected as a series from the base to the top of the core. b) PCA plot of aquatic species, axis 1 versus axis 2.

Axes		1	2	3	4	Total variance
Eigenvalues	:	0.285	0.191	0.146	0.111	1.00
Cumulative percentage variance of species data	:	28.5	47.6	62.2	73.2	
Sum of all eigenvalues	:					1.00

Table 3.1: Summary of the results of the principle components analysis (PCA) of 13 aquatic species from 43 stratigraphic samples.

Redundancy analysis of vegetation/aquatic species relationship

The eigenvalues for the first and second RDA axes were high ($\lambda_1 = 0.223$, $\lambda_2 = 0.167$) and captured 39.0% of the explained variance in the aquatic species data (**Fig. 3.8**, **Table 3.3**). The species-environment correlation for RDA axis 1 was high (0.917) and accounted for 44.1% of the variation in the species-environment relationship. The species-environment correlation for RDA axis 2 was slightly lower than axis 1 (0.808) and accounted for 33.0 % of the variation in the species environment relationship. The vegetation class "Podo. sec." (Podocarp/ Broadleaf Secondary Trees) was strongly correlated with RDA axis 1; whereas "Herb" (Herbs and Grass), and "Podo. can." (Podocarp Canopy Trees) were strongly correlated to RDA axis 2. "Disturb." (Disturbance Indicators) approximately bisects RDA axis 1 and 2, but shows a slightly higher correlation with RDA axis 2.

The cosine of the angle between species and environmental arrows (here abbreviated to COS) provides a guide to the degree of species environment correlation (ter Braak, 1987). High concentrations of *P.simplex* were typical of high percentages of "Disturb" (COS = 0.97) and "Herb" (COS = 0.86). High concentrations of *Chironomus* spp. were strongly associated with high percentages of "Disturb" pollen (COS = 0.98), but showed a higher correlation to "Podo.sec" (COS = 0.98) than to "Herb" (COS = 0.46). High concentrations of *Cricotopus* spp. and *Tanytarsus* spp. were inversely related to the percentage of "Podo.can." pollen (COS ~ -1), but showed a high positive correlation with the percentage of "Herb", "Scrub", and "Exotic" pollen (COS ~ 1, 0.9, and 0.78 respectively). Concentrations of Orthocladinae, *O. unicolor*, and Tanypodinae approach an inverse relationship to the percentage of "Exotic", "Scrub", and "Herb" pollen (COS ~ -0.6). These species show a positive correlation to both "Podo. can." and "Podo. sec." with a slightly stronger correlation to the percentage of "Podo. sec." (COS ~ 0.34 and 0.7 respectively).

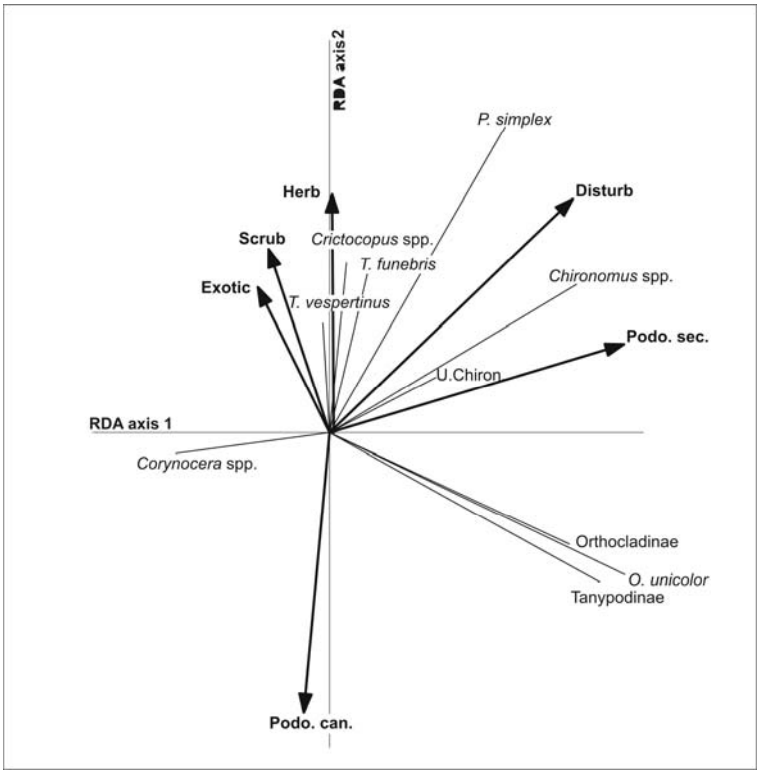


Fig. 3.8: Redundancy analysis (RDA, biplot) of aquatic taxa from the Lake Forsyth fossil record. Analysis includes 22 stratigraphic samples with pollen abundances (%) determined from the pollen record. Disturbance Indicators (Disturb.), Podocarp Secondary Trees (Podo.sec.), Podocarp/Broadleaf Canopy Trees (Podo.can.), Herbs and Grass (Herb), Low Forest and Scrub (Scrub), and Exotic Trees (Exotic). Aquatic species with actual names except for: unidentified chironomids (U. Chiron.).

	RDA		
Variable	λ1/λ2	Variance (%)	P
Disturb.	0.575	15.2	0.001
Podo.sec.	0.516	14.2	0.001
Podo.can.	0.364	10.1	0.002
Herb	0.320	9.1	0.001
Scrub	0.321	9.0	0.009
Exotic	0.161	4.7	0.172

Table 3.2: Summary of partial RDA of the faunal aquatic species assemblages from the Lake Forsyth core. The ratio of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2), and percentage variance explained by relative abundances for each pollen class. Disturbance Indicators (Disturb.), Podocarp Secondary Trees (Podo.Sec.),Podocarp/Broadleaf Canopy Trees (Podo.can.), Herbs and Grass (Herb), Low Forest and Scrub(Scrub), and Exotic Trees (Exotic).

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.223	0.167	0.08	0.021
Species-environment correlation	0.917	0.808	0.712	0.502
Cumulative percentage variance				
Of species data	22.3	39.0	47.1	49.1
Of species-environment relation	44.1	77.1	93.0	97.1
Sum of all canonical eigenvalues				0.560

Table 3.3: Summary of the results of redundancy analysis (RDA) of aquatic taxa from 22 stratigraphic samples in the Lake Forsyth core constrained to the relative abundances of 6 main pollen types.

When the species data were constrained to only one environmental variable (pollen class) (**Table 3.2**), the largest statistically significant explanatory power was captured by "Disturb" (15.2%), followed by "Podo. sec." (14.2%), and "Podo. can." (10.1%).

3.4 INTERPRETATION AND DISCUSSION

3.4.1 The early history of the Lake Forsyth Basin: a tidal estuary

Both the sedimentology and paleoecology imply that the Lake Forsyth Basin was once a tidal estuary, with a direct opening to the Pacific Ocean. This is not surprising, considering the proximity of the lake to the present coastline, and the historical accounts from the mid 19th century which mention a channel connecting Lake Forsyth to the Pacific Ocean (Soons 1998). *Chione (Austrovenus) stutchburyi* lives intertidally and in subtidal estuarine and harbour settings (Beu et al. 1990), while *Potamopyrgus pupoides* inhabits the brackish lower reaches of streams, rivers and tidal estuaries (Powell, 1979). *P. pupoides* is extant in the Avon Heathcote Estuary to the north of Banks Peninsula (**Fig. 3.1**). *Zeaflorilus parri* is a typical component of shallow, wave dominated nearshore foraminiferal assemblages around many parts of New Zealand (Hayward et. al., 1996); while an *Ammonia-Elphidium* association occurs widely around New Zealand in sheltered, intertidal mud and sand flats, and beaches (Hayward and Hollis, 1994). The overall assemblage in faunal Zone 1 probably represents mixing of death assemblages from the inner reaches of a Forsyth embayment with material from near the mouth of the bay.

The transition from a *Zeaflorilus-Ammonia-Elphidium* foraminiferal fauna in faunal Zone 1 to an exclusively *A. p. f. aoteana* fauna at the base of faunal Zone 2 (**Fig. 3.6**) indicates a partial closing off of the Forsyth Basin and a transition to a less saline and lower energy environment. The lower energy interpretation is supported by the disappearance of large shell fragments that are present at the base of the core and the gradual reduction and then elimination of sand from the sediments. The overall reduction in salinity is suggested by the reduction in foram diversity at the base of faunal Zone 2. The remaining foram species, *A. p. f. aoteana,* is widely distributed in brackish and very slightly brackish environments (Hayward and Hollis, 1994). This species is not restricted to brackish environments and may occur in virtually fresh water settings near river and stream mouths that periodically flood (Jorissen, 1988).

The reduction of salinity is also supported by both the increase in the abundance of *Chironomus* spp. head capsules and the increase in the proportion of Cyperaceae pollen in the record (**Figs 3.4**

and 3.6). The upper salinity limit for *Chironomus zealandicus* larval survival is no greater than 17.5 $^{0}/_{00}$ (Robb, 1966), demonstrating than at least part of the basin was not fully marine. The salinity records are compatible with either segmentation of environments within the basin or partial blocking (either in space or time) of the embayment by a barrier. The sediment record which comes from close to the mouth strongly suggests the latter.

3.4.2 Basal chronology and the closure of the Lake Forsyth Basin

After the disappearance of *A .p .f. aoteana* at 90 cm there is no evidence of an open marine connection. From this point on the Forsyth Basin contains a lake that was at least partially protected from a marine influence by the formation of a barrier. Barrier blocked lakes are a common phenomenon on the southern flank of Banks Peninsula (e.g., Soons et al., 1997; Shulmeister et al., 1999) and are created by littoral drifting of sediment from the south under the influence of the persistent Southland Current.

Determining the timing of formation of the barrier is more problematic. Work by Armon (1974) and Shulmeister et al. (1999) has demonstrated that the Kaitorete 'Spit' was substantially in place by about 8000 yr BP and was emplaced during the early Holocene transgression. Soons et al. (1997) dated the most recent closure of the Kaitorete Barrier to ~ 450 yr BP. This date is based on a radiocarbon age from shell hash at a marine/non-marine transition in a core from Birdlings Valley, approximately 4 km west of the Lake Forsyth Core (**Fig. 3.1**). Soons et al. (1997) believe that the Kaitoreti Barrier has opened and closed several times in the past in response to the avulsions of the Waimakariri River, north and south of Banks Peninsula. Barrier closure is only possible when the Waimakariri River flows north of the peninsula, as it does today. This is important for the Forsyth Basin because gravels can only reach the Forsyth valley mouth if the Kaitorete Barrier is closed.

An AMS radiocarbon date on a bulk sediment sample from about 1.1 m down core, yielded a calibrated radiocarbon date of 7314 to 7252 yr BP (NZA 18809). Consequently, the sandy sediments at the base of the core were probably emplaced during the final phases of the Holocene transgression (Gibb, 1986), when the Forsyth Basin was flooded by rising sea-levels. The radiocarbon date was taken from 4 cm below the transition from marine to estuarine conditions, and about 17 cm below the final disappearance of *A. p. f. aoteana* at 90 cm. It seems likely that the final closure of the Lake Forsyth Basin occurred slightly after the isolation of Birdlings Valley from the ocean (which occurred ~ 450 yr BP) as the Kaitoreti barrier would have migrated from west to east (Soons et al., 1997).

Consequently the period between the Holocene transgression and the partial closure of the basin is poorly represented in the sediment record. This could be the result of a long-term very low sedimentation rate in the bay, but is more likely to indicate that tidal sweeping of the bay prevented significant sediment accumulation. Fenster and Fitzgerald (1996) found evidence for reworking of older material following the Holocene marine transgression in a sedimentary sequence from the lower Kennebec River estuary in Maine. Modern studies in similar settings have shown that frequent periods of low deposition and erosion are common (Fan et al., 2002) and often the net sediment transport may be towards the estuary mouth (Fenster and Fitzgerald, 1996).

Other cores taken from this area provide further evidence for major periods of erosion following the last marine transgression. Soons et al. (1997) have investigated sediments in valleys on the southern side of Banks Peninsula (**Fig. 3.1**). In these valleys a fill associated with an early Holocene transgression (dated to between 8000 and 7000 yr BP) is unconformably overlain by very late Holocene (< 1000 yr BP) barrier, estuarine and lacustrine sediments. Harvey (1996) attributed unexpected old radiocarbon dates in cores taken from the shores of Lake Ellesmere (Fig. 3.1) to contamination by old carbon. However, the chronologies from the Lake Ellesmere cores closely match those of Soons et al. (1997) and the core from Lake Forsyth, suggesting that these "old" radiocarbon ages are in fact real ages.

Despite the complexity of the chronology, there is little doubt that the narrow channel separating Lake Forsyth from the ocean was in place well before the arrival of Europeans c. 1840, which is signaled by the podocarp/broadleaf pollen decline at 48 cm in the core. It is also possible that the major change in stratigraphy to increased herb detritus at 63 cm could be a signal for human arrival and there is some lag in the response of the pollen record to deforestation (this is explained in the following section).

The appearance of Tanypodinae in faunal Zone 2a possibly indicates the stabilization of Lake Forsyth as a freshwater system. There is a limited amount of data available on the salinity tolerance of New Zealand species of Tanypodinae. However, Stout (1985) noted the absence of Tanypodinae from Lake Leg of Mutton, a highly saline coastal South Island lake near Kaikoura. Stout (1985) found that in this situation, *Chironomus* spp. was the dominant taxon as is the case in the Lake Forsyth core.

3.4.3 Human impact on the Lake Forsyth catchment and adjacent areas

Pre-human vegetation

The pre-Maori settlement vegetation on Banks Peninsula has been reconstructed based on the pre-European forest distribution and the environmental preferences of the different vegetation types (Wilson, 1993). A continuous cover of podocarp-broadleaf forest comprised the emergent podocarps kahikatea (*Dacrycarpus dacrydioides* Laubenfels, Quinn and Keng), lowland totara (*Podocarpus totara* Allan), and matai (*Prumnopitys taxifolia* Laubenfels, Quinn and Keng) over a broadleaf canopy. At higher altitudes the vegetation was dominated by thin barked totara (*Podocarpus hallii* Allan) with stands of southern beech forest (mainly *Nothofagus fusca* Hook) on the southeast side of the Peninsula. This reconstruction is consistent with Holocene pollen records from Gebbies Valley on the south-west flank of the Peninsula (Soons et al., 2002) and with the findings of this study.

I interpret the consistently high values of fern spores in the Lake Forsyth record to reflect a significant contribution of river transported pollen into the Lake Forsyth Basin. Bonny (1978) found that up to 85% of the pollen found in lakes with inflowing streams has been transported by flowing water. Dunbar et al. (1997) specifically identified tree fern spores as preferentially transported via the river systems into Wellington Harbour. Many of the fern spores in the Lake Forsyth core showed signs of transport and were typically abraded in appearance, reflecting long-distance transportation. We conclude that this is a result of the dominance of fluvially transported palynomorphs in this record. Dunbar et al. (1997) also noted that changes in vegetation in response to anthropogenic influences had been "diluted" by the mass of palynomorphs recycled from soils and those sourced from distal parts of their catchment that escaped clearance. Consequently there was a delayed response to deforestation by pollen records from cores taken from settings with a high fluvial contribution.

Human disturbance in the catchment

Maori disturbance.

New Zealand has a relatively short history of human occupation. The Maori people arrived in New Zealand from Eastern Polynesia between 1200 and 1400 AD (McGlone and Wilmshurst 1999). Pollen analysis from numerous sites around New Zealand (e.g. McGlone et al., 1995; Elliot et al., 1997; Horrocks et al., 2002) indicate that this first wave of human colonizers dramatically reduced

the area of native forest cover. The Maori people used fire during moa hunting (Scott, 1999), as a means of land clearance, and to encourage the growth of bracken (*Pteridium esculentum* Forster) (McGlone, 1989). Consequently a Maori disturbance signal in the pollen record can be inferred by a decline in canopy tree pollen, a major increase in the quantity of *P. esculentum* spores, an influx of charcoal particles, follwed by the appearance of pollen from colonizing species such as *Coriaria* spp. (McGlone and Wilmshurst, 1999).

Radiocarbon dating of moa-hunting sites suggests the presence of Maori settlers on Banks Peninsula by 1300 AD (Challis, 1995). It has been predicted that as much as a third of the pre-Maori forest cover was destroyed prior to the arrival of Europeans in the area in 1840 (Soons et al., 2002). Pollen analysis of a core from Travis Swamp, Christchurch (**Fig. 3.1**) (McGlone, 1995; cited in McGlone and Wilmshurst, 1999) shows evidence for major Maori deforestation beginning between 1218 and 1397 AD.

There is no definitive evidence in the Lake Forsyth pollen record for significant pre-European deforestation. There are several very minor peaks of *Pteridium esculentum* between 120-90 cm core depth, and there is an isolated increase in Asteraceae and *Leptospermum/Kunzea* spp. which is accompanied by a minor decline in the abundance of canopy tree pollen at about 80 cm depth. In the absence of major changes disturbance indicating taxa, the relative lack of charcoal, and the propensity of eastern South Island, New Zealand to be subject to natural disturbance due to drought, the presence of a Maori disturbance signal is inconclusive.

European forest clearance and pastoral farming.

The widespread deforestation of Banks Peninsula, and the subsequent conversion of large tracts of land to pastoral farming after 1860 is well documented (Petrie, 1963). The period of deforestation is represented in the pollen record by the major decline in canopy tree pollen, accompanied by a peak in charcoal and *P. esculentum* at the end of pollen Zone II. The establishment of grassland and the planting of exotic trees is evident in pollen Zone III, and is expressed as a major increase in Poaceae pollen. Foweraker (1927) mentions the planting of large stands of mixed conifers (including *Pinus* spp.) in the Canterbury region around 1870. Dunbar et al. (1997) found there was a delay of 25 years between the first planting of *Pinus radiata* D.Don in 1865 in Wellington, New Zealand, and its appearance in the pollen record about 1890. The first appearance of *Pinus* spp. pollen in the Lake Forsyth record post dates deforestation, which was largely completed by 1880 (Petrie, 1963). It seems reasonable to assume a similar delay in the appearance of *Pinus* spp. in the Lake Forsyth pollen record, and a date of 1895 is assigned to the first appearance of *Pinus* spp. in the record (**Figs**

3.4 and **3.6**).

3.4.4 The influence of land-use changes on the aquatic ecosystem.

Results from redundancy analysis (RDA) (**Fig. 3.8**, **Tables 3.2** and **3.3**) reveal a strong correlation between changes in regional vegetation and the concentrations of the main aquatic taxa. It appears that deforestation resulted in conditions in the lake that encouraged the appearance, and increase in abundance of the aquatic invertebrate taxa, particularly *Chironomus* spp. beginning in faunal Zone 2a and peaking in faunal Zone 3. Results from the principle components analysis (PCA) (**Fig 3.7**) show a period of dramatic change in the aquatic species assemblage between ~43 cm and 20 cm. This corresponds with a pulse of increased diversity between ~ 50cm and 35 cm, and the period of deforestation recorded in the pollen record in pollen Zone II (**Figs 3.4** and **3.6**).

This change in the aquatic taxa probably reflects an initial low input of nutrients into the lake coupled with a reduction in salinity. This is supported by the appearance of low concentrations of colonies from *P.simplex* at the faunal Zone 2/Zone 3 transition. Yasuda et al. (2000) discovered a similar increase in *Pediastrum* following deforestation in a core from the Ghab Valley in Northwest Syria. Patterson et al. (2002) also found a strong correlation between *Pediastrum* abundance and the levels of other high nutrient proxies in a core from Swan Lake, Ontario. Historical records state that there was at least a temporary connection between Lake Forsyth and the ocean up until 1843 (Soons, 1998). Frequent intrusions of salt water until this time would have prevented the proliferation of *Pediastrum* which only blooms in freshwater.

Salinity was probably the main determinant of aquatic biological diversity prior to the isolation of the lake from the ocean, and the initiation of deforestation. These changes temporarily changed the aquatic system to one that was primarily driven by the availability of nutrients and dissolved oxygen. This initial reduction in salinity favoured the survival of the Tanypodinae and larvae from the caddis fly *Oecetis unicolor*. Both of these taxa are a common component of many of New Zealand's freshwater oligo-mesotrophic lakes (Stark, 1981; Timms, 1982; 1983; Schakau, 1991).

The massive increase in the abundance of *P.simplex* and the disappearance of Tanypodinae and *O. unicolor* in faunal Zone 4 suggests a continuation of the low salinity phase, with a switch to a highly productive system. Both the Tanypodinae and *O.unicolor* are absent from shallow highly productive lakes (Stark, 1981; Timms 1982 and 1983; Schakau, 1991). Patterson et al. (2002) proposed that a similar *Pediastrum* peak in a core from Swan Lake Ontario reflected the increased use of chemical based fertilizers after World War 2. The *Pediastrum* 'bloom' postdates 1895 AD, a date inferred by

the appearance of *Pinus* spp. in the record. An estimate based on constant sediment accumulation and slight compaction places the *Pediastrum* peak at 1910 to 1930. Intensive use of aerial topdressing did not occur in New Zealand until 1950 (Alexander and Tullett, 1967). Main (2002) also mentions that the first *Nodularia spumigena* bloom was reported in Lake Forsyth in 1907, well before the intensive use of fertilizers after World War 2. It seems likely that the increased nutrient input resulting from increased erosion following deforestation, coupled with the increase in dairy farming in the area in the early part of the 20th century (Main, 2003) was enough to stimulate a major *Pediastrum* peak, and initiate blooms of *N. spumigena*.

The introduction and proliferation of the black swan (*Cygnus atratus* Latham) in New Zealand in the early 19th century (Mitchell and Wass, 1996) may also have contributed to high nutrient levels and algal blooms in the lake. Waterfowl faeces contain a low ratio of N to P (Mitchell and Wass, 1995) which may also favour the proliferation of cyanobacteria in lakes where the faecal component of the nutrient load is large.

Increased catchment erosion also increased the sedimentation rate in the lake from a pre 1840s rate of 0.88 mm/yr to 3.7 mm/yr, a 4-fold increase. It does not appear that an increased sedimentation rate by itself had a negative affect on the survival of aquatic invertebrate taxa. It is quite possible that an input of fine material favoured *Chironomus* spp., which has a preference for a fine muddy substrate (Boubee, 1983). Warwick (1980) also proposed that increased levels of sediment input may benefit predatory chironomids (Tanypodinae) when other invertebrates are forced out of the sediments and become vulnerable to predation.

The major decline in the abundance of both *P. simplex* and *Chironomus* spp. is probably indicative of a recent increase in salinity. Lake Forsyth is artificially opened to prevent flooding of the Christchurch-Akaroa highway after periods of high rainfall (Soons, 1998). During the period of 1999 to 2003 salinity reached extreme values of up to 11 $^{0}/_{00}$ during the spring and autumn, following the opening of the lake (Canterbury Regional Council, unpublished data). Robb (1966) found that salinities of this magnitude increased the mortality of *Chironomus* spp. larvae. It is likely that such high salinities are responsible for the low chironomid diversity and may have a detrimental effect on other aquatic flora and fauna. Schallenberg and Burns (2003) argue that even small salinity increases that raise the salinity to > 1.2 psu (approximately 1.2 $^{0}/_{00}$) can dramatically affect the biodiversity and ecosystem functioning of coastal brackish lakes. Increased salinities may also favour the massive blooms of *N. spumigena*. *N. spumigena* not only benefits from increased nutrient levels, but is also halotolerant (Mazur, 2003). Increased nutrient input coupled with increased salinity may have allowed *N. spumigena* to out-compete other species of planktonic algae, including

P. simplex, resulting in algal blooms. Extensive cyanobacteria blooms seriously affect water quality in that they cause deoxygenation and produce hydrogen sulphide (Mazur, 2003). Consequently, frequent *N. spumigena* blooms may have accelerated the decline in water quality.

3.5 CONCLUSIONS

3.5.1 Directions for future management

This paleolimnological study shows the natural development of the Lake Forsyth basin from a tidal coastal embayment ~7000 years BP to a barrier blocked lake, partially isolated from the ocean about 500 years BP. The lake was permanently isolated from the ocean after the arrival of Europeans in the area c. 1840. It appears that human activities over the last 150 years have resulted in three main effects that could be distinguished from signals of natural coastal evolution; salinity changes, increased sedimentation rate, and increased nutrient inputs. A program for the future restoration of this lake should target these areas. The following section examines these points in more detail.

Deforestation led to an increased overland flow and an increased input of freshwater into the lake. As the start of deforestation coincided with the natural isolation of the lake from the ocean it is difficult to determine how much of this salinity reduction was natural and hence set a baseline level for salinity in this lake. It is certain, however, that the recent practice of artificially breaching the gravel barrier separating the lake from the ocean has led to large salinity fluctuations that have a detrimental effect on most of the aquatic fauna. It is necessary to maintain lake levels to prevent flooding of nearby roads and farmland. An alternative method of lake level control that prevents backwash of saline water into the main basin and allows the return migration of eels from the ocean should be investigated.

It is also quite clear that land clearance and ensuing pastoral farming practices have led to an increase in the inflow of nutrients and suspended sediments, resulting in a 4-fold increase in sedimentation rates and blooms of the toxic cyanobacteria *Nodularia spumigena*. A primary directive for future restoration of this system should be watershed nutrient and sediment reduction strategies. The restoration of the wetland at the head of the lake may serve as a natural filter to aid the removal of nutrients and suspended solids transported from the catchment via the Okana and Okuti rivers. Replanting of the steep slopes to the north and south of the lake may also serve to reduce sediment input. The lake may take some time to respond to these measures; since Lake

Forsyth is shallow (< 4 m maximum depth) it is likely that nutrients stored in the surface sediments will be re-suspended by wind disturbance.

3.5.2 Chironomids as a proxy for environmental change in coastal brackish lakes.

The low taxonomic richness of chironomids in this setting means that it difficult to disentangle signals of salinity and productivity from the relative abundance of chironomid taxa alone. Head-capsules belonging to the genus *Chironomus* were most common in this core. Larvae from this genus (particularly *Chironomus* sp. a) are tolerant of both saline and eutrophic conditions. This may also have implications for the development and application of chironomid-based inference models for lake production or trophic level (this is discussed further in **Chapter 9**). *Chironomus* head-capsule concentrations seem to be most useful as indicators of salinity in this case. Care should be taken with such interpretations as head-capsule concentrations are also effected by sedimentation rate. A high sedimentation rate may result in a decrease in the chironomid head-capsule concentration. The fact that the head-capsule concentration increases with an increased sedimentation rate (the upper 40cm of the core) and coincides with the disappearance of foraminifera and the arrival of truly freshwater taxa (*Pediastrum*, *Oecetis unicolor*) suggests that head-capsule concentration is a true indicator of the abundance of *Chironomus* larvae in the lake in the past. The chironomid data is most useful in this setting when compared with the information provided by the other proxies. The presence of the remains of caddis fly larvae (Trichoptera) and cases provide an upper limit for lake productivity in this case. Larvae from *Oecetis unicolor* are absent from eutrophic lakes, but can tolerate mesotrophic conditions.

Fossil Pigment analysis (chlorophyll, carotenoids) may be the most useful tool for the reconstruction past lake production in this setting. Diatom-based transfer-functions for lake production (chlorophyll *a*) and salinity have also been recently developed (Reid, 2005). However I believe that similar problems involving the separation of the salinity and lake production signals may arise with this proxy as well (see **Chapter 4** for further discussion of this matter).

CHAPTER 4: THE DEVELOPMENT OF CHIRONOMID-BASED INFERENCE MODELS FOR PALEOENVIRONMENTAL RECONSTRUCTIONS

PART I: INTRODUCTION AND METHODS

4.1 INTRODUCTION

4.1.1 Background

It was realised very early in human history that the fossilised remains of certain plants or animals could provide information on past environmental conditions. The Greek philosophers Xenophanes (570 - 480 BC) and Herodotus (484 – ca. 425 BC) proposed that the presence of seashells many kilometres inland from the sea indicated that land was once underwater (Imbrie and Newell, 1964). More recently, in the early nineteenth century Gideon Mantell recognised that the fossil parts of plants and trees he found in a quarry in Sussex, England were quite different to those found in the region at the time. Mantell confirmed his suspicions that these plants were of tropical affinity by comparing the fossil material with specimens in the British Museum and with living plants in hothouses (Freeman, 2004). This represents one of the earliest published examples of a paleoclimate reconstruction. The simple premise that fossil organisms or assemblages lived in similar conditions to their modern equivalents is probably the most important underlying assumption in the science of paleoecology.

Until later in the twentieth century reconstructions of past environmental conditions based on the fossil record were usually limited to qualitative statements. Although fossil assemblages were studied quantitatively with individual fossil foraminifera, pollen, diatoms being counted, the environmental inferences based on these assemblages were usually restricted to broad statements of faunal affinity or general environmental conditions ("freshwater", "warming", "cool", etc.) (e.g. Murray, 1965; Baker, 1970; Watts, 1970). The development of foraminifera-based transfer functions for ocean surface temperatures and salinity by Imbrie and Kipp (1971) represented a major step forward in the field of Quaternary paleoenvironmental recontructions. Imbrie and Kipp (1971) used modern planktic Foraminifera assemblages from 61 core tops in the Atlantic Ocean (called a modern training set) to develop transfer functions or calibration functions that enabled the reconstruction of specific values (with error margins) for sea surface temperature and salinity.

Since the pioneering work of Imbrie and Kipp (1971) there have been many developments in this field. The numerical techniques and software packages for exploratory data analysis and inference model development have continued to evolve (e.g ter Braak and Juggins, 1993). Transfer functions have been developed for a wide range of biological proxies, including diatoms (e.g. Werner and Smol, 2005), pollen (e.g. Seppa et al., 2004), Foraminifera (e.g. Barrows and Juggins, 2005), chironomids (e.g. Larocque et al., 2001), and Cladocera (e.g. Lotter et al., 1997). These transfer functions have been applied to sedimentary sequences in order to investigate past climate change (e.g. Brooks and Birks 2000; Langdon et al., 2004) and human impact on aquatic ecosystems (Quinlan and Smol, 2002; Heinrichs et al., 2005). So far most of this research has been conducted in the Northern Hemisphere. Large training sets have been developed for many of these proxies, particularly diatoms (e.g. Cameron et al., 1999) and chironomids (e.g. Lotter et al., 1999). Quantitative reconstructions have also been compared with actual climate data (e.g. Larocque and Hall, 2003) and lake monitoring data (e.g. Hausmann and Kienast, 2006).

This discipline is still in its infancy in the Southern Hemisphere. One of main limiting factors has been a poor knowledge of the taxonomy of many of the biological groups coupled with the logistical difficulties of sampling in Africa and South America (e.g Verschuren and Eggermont, 2006). Recent developments in the taxonomy of many of the useful proxy groups (particularly the Chironomidae, e.g. Boothroyd, 1994, 1999, 2002; Cranston, 1996) has created the opportunity to use these groups to develop quantitative inference models. The urgency for developing paleoclimate records in the Southern Hemisphere has been fuelled by the need to develop and assess global climate models that will enable the prediction of future climate change scenarios. Increasing populations, developing technology and changing farming practices have increased pressure on water resources and raised concern over the future management of aquatic ecosystems in the Southern Hemisphere. Detailed lake monitoring has only started in the last few decades in many countries in the Southern Hemisphere (e.g. Taylor and Smith 1997; Verschuren, 2003). Reconstructions of past changes in lake productivity (nutrients (TN and TP) and chlorophyll *a*) and conductivity provide valuable information on natural and human induced environmental changes.

4.1.2 Paleoclimate proxies in the Southern Hemisphere

Large Foraminifera training sets extend into the Pacific Ocean (Barrows and Juggins, 2005) and enable the reconstruction of past sea surface temperatures (SSTs). On land however, it is a different story. There are excellent ice core records from Antarctica (Jouzel et al., 2006) but fossil pollen has

remained the main paleoclimate proxy in South America (e.g. Ledru et al., 2006), New Zealand (e.g. Vandergoes et al., 2005), Australia (Kershaw, 1986; Colhoun et al. 1999) and Africa (Marret et al., 2006). There are many problems with inferring past climate from fossil pollen, including taphonomy, and the fact that vegetation changes may be caused by a number of environmental factors unrelated to climate (Chapin et al., 1993). Tree ring records provide high resolution records, which can be more easily related to climate, but continuous records span a short period of time (< 2000 years) in the Southern Hemisphere (Cook et al., 2002).

Chironomid-based salinity transfer functions in Africa have been used to infer moisture balance variations over the past 1100 years (Verschuren et al., 2000a). Diatom-based salinity transfer functions in Australia have also been used to derive long-term climate records (Gell et al., 2005). In New Zealand, transfer functions have been developed for phytoliths (Prebble et al., 2002) and testate amoebae (Wilmshurst et al., 2003) while bioclimatic modelling approaches have been applied to beetles (e.g. Marra et al. 2004). For some of these proxies (e.g. phytoliths) the inference of climate parameters from the data is not straightforward, while with others (e.g. testate amoeba) reconstructions appear to be affected by preservation biases.

Other proxies that have been used to develop long term climate records in the Southern Hemisphere are also difficult to interpret. $\delta^{13}C$ isotopic data from speleothems is representative of changes in vegetation cover, but the interpretation of $\delta^{18}O$ values in the speleothem records is extremely complex (e.g. Hellstrom et al., 1997; Xia et al. 2001, Williams et al., 2005). Changes in depositional conditions, and in the $\delta^{18}O$ of meteoric waters (and therefore the cave seepage waters), also influence the $\delta^{18}O$ of speleothem calcite, and in many situations are likely to obscure the temperature-controlled signal (Hellstrom et al., 1997). Paleo equilibrium line altitudes (ELAs) and moraine positions have also been used to infer past temperature fluctuations (e.g. Benn et al., 2005; Anderson and Mackintosh, 2006). However, changes in both temperature and precipitation can cause shifts in the position of the ELA (e.g. Rother and Shulmeister, 2006).

4.1.3 Proxies for environmental changes in New Zealand lakes

Chironomids:

One the earliest paleolimnological studies in New Zealand was performed by Deevey (1955) who examined lake sediments from Pyramid Valley Swamp in the South Island (**Fig. 4.1**). Deevey used a variety of biological proxies to infer environmental changes resulting from human impact on the

surrounding landscape following the immigration of the Polynesians between 1200 and 1400 AD (McGlone and Wilmshurst 1999). This study also involved the examination of the chironomid fauna, but was hindered by limited taxonomic knowledge of this group, and the lack of ecological information. A later study by Boubée (1983) also focused on the chironomids. The study by Boubée (1983) was the first worldwide to introduce surface-sediment calibration data sets and multivariate statistics to chironomid paleoecology. Boubée (1983) collected chironomid remains and environmental data from 12 North Island Lakes. Fossil chironomid data from a sediment core spanning 17,000 years from Lake Maratoto (**Fig. 4.1**) were plotted as a time series on a principle components analysis (PCA) of chironomid remains from the surface sediment samples. Thus Boubée (1983) was able to describe long-term environmental changes in this lake including lake-level fluctuations. Schakau (1993) also sampled the surface sediments of 35 lakes for chironomid remains. With the benefit of hindsight, this early study by Schakau suffered from several problems that made it difficult to extract useful information on the controls of temperature and trophic status on New Zealand chironomids. The 35 lakes sampled by Schakau (1993) were all situated below the tree-line and were mostly oligotrophic; therefore her lakes were not evenly spaced over long environmental gradients. Schakau (1986; 1990; 1993) interpreted an increased abundance of head-capsules belonging to the Chironomini in the last 1000 years in Lake Taylor and Lake Grassmere to be indicative of nutrient enrichment following forest clearance. However, she was not able to confidently identify the head-capsules from the genus *Chironomus* to species level. As I discussed in Chapter 2 there are actually nine species of *Chironomus* on the New Zealand mainland. Not all are indicators of nutrient enrichment (see discussion in **Chapter 5**)

Fossil pigments:

Photosynthetic pigments preserved in lake sediments can be used to provide a proxy of past lake production. Different types of photosynthetic pigments are characteristic of certain taxonomic classes of algae with, myxoxanthophyll and canthaxanthin being typical of the toxin producing, bloom forming cyanobacteria (blue-green algae) (Rowan, 1989). Interpretation of sediment pigment data can be complicated by factors such as photo-degradation of pigments in the water column and transformation of pigments within the sediments (Carpenter et al. 1988; Steenbergen et al., 1994). Despite this fact, changes in the fossil pigment stratigraphy from Lake Okaro (**Fig. 4.1**) in New Zealand (Downes and Hawes, 1994) corresponded well with the documented information on algal species changes for this lake. Gall and Downes (1997) produced pigment stratigraphies from four

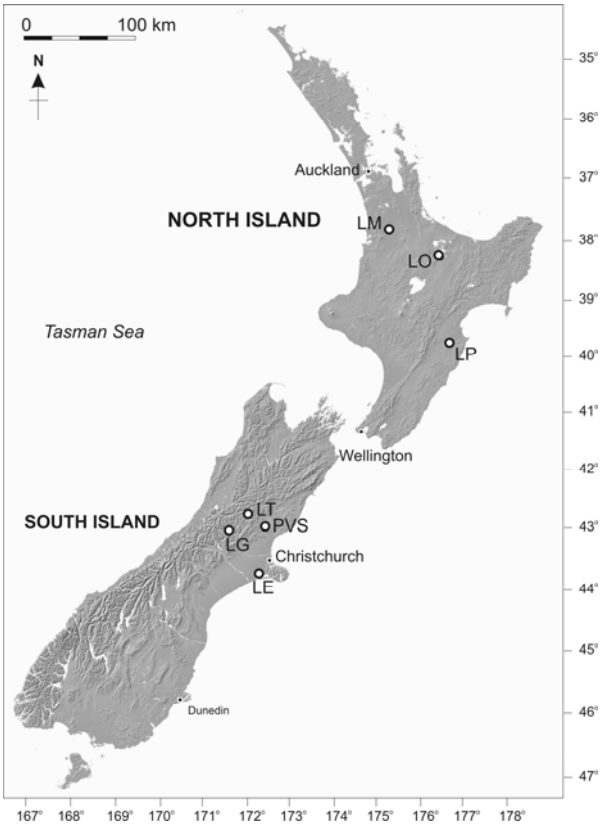


Fig. 4.1: Location of some important paleolimnological studies in New Zealand that have been mentioned in the text. PVS = Pyramid Valley Swamp, LM = Lake Maratoto, LT = Lake Taylor, LG = Lake Grassmere, LO = Lake Okaro, LE = Lake Ellesemere, LP = Lake Poukawa.

lakes in the North Island of New Zealand. These lakes range in productivity from oligotrophic to eutrophic. Three of the lake records extended back to the early 19th century, which is prior to the initiation of intensive pastoral farming in New Zealand ca. 1920 AD (Glasby, 1991). All three pigment records contained higher concentrations of algal pigments typical of the cyanobacteria after 1940. This trend generally agrees with historical observations, however pigment concentrations that coincide with the the period between 1988 and 1995 are at odds with actual measured pigment concentrations in the water column. Gall and Downes (1997) suggest that this may be due to the effect of the limited water column sampling versus the integrating effect of sediment accumulation on pigment concentrations. Harvey (1996) also performed fossil pigment analysis of sediments from the shores of Lake Ellesmere as part of a diatom-based paleoecological study of this lake (this is described in more detail in the following section).

Diatoms:

Harper et al. (1986) produced a diatom stratigraphy from a sediment core from Lake Poukawa in the North Island (**Fig. 4.1**). The main focus of this study was the effect of the tephra fallout into the lake on diatom productivity. The draining of the swamp ca. 1931 was reflected in the diatom record by

an increased abundance of the genus *Fragilaria*. Harvey (1996) studied the diatom assemblages from 4 short cores from around the shoreline of Lake Ellesmere (**Fig. 4.1**) and used the environmental tolerance of the fossil diatom genera, coupled with physical and chemical analyses of the sediments (fossil pigments, loss-on-ignition, phosphorus and nitrogen) to infer past environmental changes (e.g. salinity, productivity) within this lake for at least the last 1000 years. Harvey argued that this lake has been eutrophic for most of its history, even prior to the arrival of Europeans and the initiation of intensive farming practices. However, evidence for long-term eutrophic conditions in this lake is not conclusive. The different lines of evidence (diatoms, chemistry etc.) are not consistent within each core, and the general trends (eutrophication, oligotrophication) are not consistent between cores. Harvey (1996) based his ecological interpretations on the environmental tolerances of equivalent diatom genera from the Netherlands, based on publications by Vos and De Wolf (1993) and Van Dam et al. (1994).

Cochran (2002b) produced a diatom-based conductivity transfer function which has been applied to coastal sedimentary records to produce evidence for coastal uplift due to earthquakes in the past (Cochran 2002a). Reid (2005) produced diatom-based transfer functions for electrical conductivity (EC), chlorophyll *a* (Chla), total phosphorus (TP), dissolved reactive phosphorus (DRP) and pH from a 53 lake training set from the North and South Island of New Zealand. Despite the fact that these inference models were apparently robust (high r^2, low root mean squared error of prediction (RMSEP)), TP, DRP and Chla are highly correlated in the training set, and EC (which produced the most robust model) is highly correlated to temperature. The environmental gradients for Chla and EC were also highly correlated in a constrained correspondence analysis (CCA) of the diatom species data and the environmental data. This means that we cannot be sure whether the Chla and EC transfer functions are reconstructing EC, Chla (or changes in both).

4.1.4 Development of New Zealand chironomid-based transfer functions

The paucity of quantitative paleoenvironmental proxies in the Southern Hemisphere provided an impetus to create New Zealand chironomid-based transfer functions.

New Zealand paleoclimate history has become a focus for international studies, because New Zealand is seen as a good distal location to test paleoclimate hypotheses developed from Northern Hemisphere data (e.g. Broecker, 1997). This is particularly true for the time interval from the last glacial maximum (LGM) (ca. 21,000 years ago) to the start of the present interglacial (ca. 13,000 years ago). In New Zealand, rigorous scientific monitoring of lakes and estuaries only extends back

as far the early 1980s (Taylor and Smith, 1997) and there are few continuous records of physiochemical parameters. The limited extent of the monitoring data from New Zealand lakes means that we have a limited understanding of how these ecosystems change over time and how they respond to human impact. Chironomid-based inference models for temperature and lake productivity/chemistry would contribute valuable data that would contribute to our understanding of New Zealand aquatic ecosystems and the climate of this region. The previous studies conducted in the Northern Hemisphere have shown that chironomids can be used as proxies for temperature (e.g. Brooks and Birks, 2000) and to quantify the effects of human activities on aquatic ecosystems (Quinlan and Smol, 2002).

This chapter outlines the development of New Zealand chironomid-based transfer functions from a training set of 46 lakes. The results published here are a modified version of a paper published in the Journal of Paleolimnology in 2006 (Woodward and Shulmeister, 2006; **Appendix D**). Since the publication of this paper it has become possible to sub-divide the ubiquitous chironomid genus *Chironomus* into Chironomus sp. a and *Chironomus* spp. (see **Chapter 2**). The numerical analyses were therefore performed again to see what effect this had in the exploratory data analyses, and how these new data affected the inference models. An outline of the methodology is provided here in Chapter 4, the results for the exploratory data analyses and transfer function development are provided in Chapters 5 and 6 respectively.

4.2 Description of sites studied

The training set comprised 46 lakes located in the North and South Island of New Zealand (38.04ºS to 45.12 ºS latitude, 167.49 ºE to 176.16 ºE longitude) (**Fig. 4.2**, **Table 4.1**) The climate in this region is generally mild and oceanic. However, there are large temperature and precipitation gradients in the New Zealand region, particularly in the South Island. This is a product of the rugged topography of the Southern Alps and the influence of this mountainous terrain on the predominantly westerly airflow over the southern part of the country (Sturman and Wanner 2001). Orographic uplift of the airflow off the Tasman Sea results in an extreme contrast in average rainfall between the western and eastern sides of the mountains. Average annual precipitation near the divide on the western side of the Southern Alps can reach over 10,000 mm, while the eastern coastal plains and mountain basins receive an average annual rainfall of 600 mm (Griffiths and McSaveney

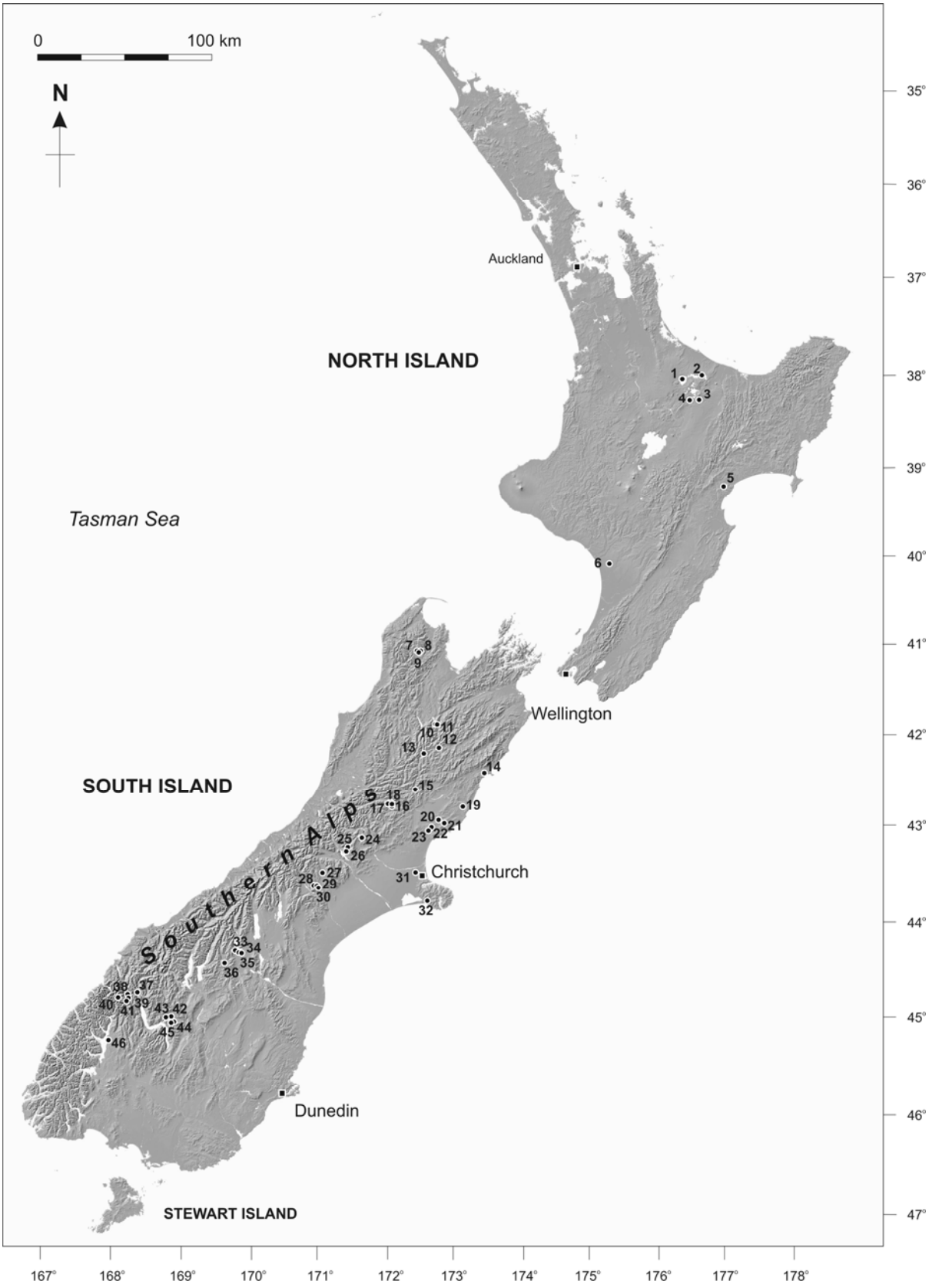


Fig 4.2: Map showing the distribution of the 46 study lakes in New Zealand. Numbers refer to lakes listed in Table 4.1.

1983). Elevation of the sample sites ranges from 20 to 1880 m a.m.s.l. (above mean sea level), corresponding to estimated late summer (February) mean air temperatures of 8.2 to 18.1 ºC (**Table 4.1**).

The catchment vegetation of all the sample locations in the North Island and those located on the eastern coastal plains and foothills (below ~ 450 m a.m.s.l.) of the South Island has been subjected to intensive human modification. The original podocarp/broadleaf forest (e.g. *Podocarpus* spp., *Prumnopitys* spp., and *Dacrydium cupressinum*) cover in these areas has been largely cleared, firstly by Polynesian settlers, and more recently by Europeans to make way for pastoral farming (Ogden et al. 1998). Catchment vegetation of the lakes in these areas now comprises low scrub (e.g. *Discaria toumatou*, *Coprosma* spp., and *Leptospermum* spp.), exotic trees (e.g. *Pinus radiata*), and introduced pasture grasses (e.g. *Pennisetum clandestinum*).

At higher altitudes up to the tree-line (~1000 to 1300 m a.m.s.l.) the natural vegetation comprises beech forest (four endemic species of *Nothofagus*) except for in the mid-central South Island 'Beech Gap' where podocarp/hardwood forests (e.g. *Podocarpus* spp.) give way to other conifers (*Libocedrus* spp., *Phyllocladus* spp., and *Halocarpus* spp.) at higher altitudes up to the tree-line. This natural forest cover now only exists in conservation reserves, and in remote, rugged un-farmed areas. Cleared forest has been replaced by indigenous grassland (montane tussock-land; e.g. *Poa* spp.). Large tracts of this land are now used for low-density sheep farming. Above the tree-line, forest and scrub gives way to sub-alpine tussock (e.g. *Chionochloa* spp.) and other alpine flora (e.g. Asteraceae, Gentianaceae, and Ranunculaceae). Introduced grasses and composite weeds have also invaded this zone but less successfully than at lower elevations.

4.3 FIELD METHODS AND LABORATORY ANALYSES

A total of 46 lakes, selected to maximize the gradients of trophic status and temperature, were sampled in New Zealand during the summers (December to February) of 2002/2003, 2003/2004, and 2004/2005 (**Fig. 4.2** and **Table 4.1**). Surface sediment samples, physical measurements and water chemistry for the lakes sampled in 2002/2003 were a product of a diatom training set developed by Reid (2005).

Prior knowledge of the trophic status of potential lakes was obtained from local government monitoring records (e.g. Christchurch Regional Council, unpublished dataset), data obtained from

previous studies on New Zealand aquatic ecosystems (e.g. Timms 1982; 1983; Stout, 1985) and the previous investigations of New Zealand chironomid ecology by Boubee (1983) and Schakau (1993).

Small (median 0.180 km^2), shallow (median 10.2 m depth) lakes were preferentially sampled to ensure a close relationship between water temperature and air temperature. Ideally, the sampling of deep (> 30 m) lakes should be avoided to eliminate the effect of hypolimnetic anoxia on the chironomid species assemblages (Little and Smol, 2001). All efforts were made to select lakes within these criteria, but due to the lack of bathymetric data for New Zealand's high altitude lakes, some of the high altitude lakes were deeper (**Table 4.1**). A preliminary ordination of the species and environmental data indicated that depth was not a significant ($P < 0.01$) driver of species variation in the training set, even when these deep lakes were included.

At each lake, maximum depth was determined using bathymetric maps and a NorCross Hawkeye® DF2200PX portable depth finder. When bathymetric maps were not available, multiple transects were taken to determine the deepest point of the lake. At the deepest point, two surface water samples (0-1 m) were collected in acid-washed 500 ml Nalgene bottles, which were rinsed with lake water. Surface water temperature, pH, and conductivity (Cond) were measured using a Hannah® HI 8424 pH meter and thermometer, and a Eutech® Cyberscan Con 20 conductivity meter. One of the surface water samples was immediately filtered using a syringe and Whatman® 25mm Ø GF/F glass microfibre filters. Filters were wrapped in foil and kept for subsequent analysis for chlorophyll *a* (Chla) concentration determination, which was conducted in the Environment Canterbury laboratory in Christchurch, New Zealand. The 500ml filtered and unfiltered samples were kept frozen until analysis at the Environment Chemistry Laboratory, Massey University, Palmerston North, New Zealand. Samples were analysed for ionic concentration (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, SO_4^{2-}) and nutrients (reactive nitrogen (NO_x-N), reactive phosphorus (RP), total nitrogen (TN), total phosphorus (TP)), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and total carbon (TC). Water samples collected by Michael Reid in 2002/2003 (Reid 2005) were only analysed for nutrients (NOx, RP, TN, TP) and Chla. Even though other studies have shown that oxygen concentrations may have an influence on chironomid distribution (e.g. Little and Smol, 2001), dissolved oxygen was not measured during this study. Because the equipment often had to be carried in long distances, some measurements were sacrificed because the 'cost' outweighed the possible benefit. Previous studies (e.g., Little and Smol , 2001) have shown that it is important to gauge how dissolved oxygen varies with depth and time (the period of hypolimnetic anoxia) in order to provide meaningful data for chironomid-based inference models. This was not possible as some of the more remote lakes could only be visited once. A summary of the physical measurements and

Table 4.1: Summary listing some important variables pertaining to lake location, morphology, production, chironomid head-capsule count (HC) and taxonomic richness (# Taxa). Cond = Electrical conductivity, Chla = concentration of chlorophyll *a*. Shaded cells highlight low head-capsule counts.

Lake nr	Location	Lat (^oS)	Long (^oE)	Altitude (m)	Feb Mean (^oC)	Water temp. (^oC)	Lake Area (Km^2)	Depth (m)	Chla (µg/L)	HC Count	# Taxa
1	**Lake Rotorua N**	38.04	176.16	280	17.8	19.2	79.780	20.50	32.10	67	8
2	**Lake Rotoehu**	38.01	176.31	295	17.6	20.5	8.110	10.00	25.00	114.5	9
3	**Lake Rerewhakaaitu**	38.17	176.29	435	16.8	18.1	7.470	14.00	3.60	216.5	14
4	**Lake Okaro**	38.17	176.23	412	17.0	19.1	0.280	16.00	5.79	63	7
5	**Lake Tutira**	39.13	176.53	150	18.1	20.5	1.470	40.00	3.82	119.5	10
6	**Lake Dudding**	40.06	175.16	86	17.5	18.3	0.130	12.00	19.11	68	9
7	**Iron Lake**	41.06	172.36	1463	10.2	14.5	0.068	21.00	0.50	89	6
8	**Lake Sylvester**	41.06	172.37	1333	10.9	14.5	0.266	24.20	0.40	56.5	9
9	**Little Sylvester Lake**	41.06	172.37	1333	10.7	14.8	0.076	14.00	0.40	59.5	14
10	**Rainbow Skifield W**	41.52	172.51	1690	9.8	14.3	0.052	10.10	0.70	337	8
11	**Rainbow Skifield E**	41.53	172.52	1479	10.5	14.2	0.028	4.50	0.20	111.5	7
12	**Lake Sedgemere**	42.08	172.54	1008	12.9	14.7	0.080	1.30	0.50	235.5	16
13	**Princess Bath**	42.11	172.41	1757	9.0	12.8	0.070	15.50	2.30	81	3
14	**Lake Rotorua S**	42.24	173.34	20	17.3	29.4	0.550	2.08	15.30	104	13
15	**Horseshoe Lake**	42.35	172.31	468	15.4	20.5	0.040	10.30	0.40	331.5	13
16	**Lake Taylor**	42.46	172.13	588	14.1	15.9	1.850	35.00	2.27	134.5	11
17	**Lake Mason**	42.44	172.10	329	14.1	15.3	1.000	37.00	1.11	53.5	14
18	**Lake Sheppard**	42.45	172.15	587	14.6	16.8	1.150	17.00	8.10	51.5	12
19	**St Annes Lagoon**	42.46	173.16	33	17.1	25.9	0.200	1.00	7.30	95	7
20	**Mill**	42.55	172.55	146	16.6	22.8	0.060	2.70	9.80	76	9
21	**Lake Greta**	42.57	172.58	183	16.3	22.0	0.020	3.10	8.90	17	4
22	**Glen**	43.01	172.47	78	16.8	19.2	0.070	1.40	41.30	534	14
23	**Hut**	43.02	172.46	71	16.9	17.4	0.100	5.00	4.40	70	6
24	**Lake Pearson**	43.06	171.46	611	14.6	16.0	1.790	15.00	2.36	156	8
25	**Mystery Tarn**	43.12	171.34	854	13.3	18.2	0.020	8.00	0.40	425	16
26	**Lake Evelyn**	43.15	171.32	580	14.7	17.5	0.150	3.00	0.60	208	12
27	**Lake Heron**	43.29	171.10	691	13.7	15.6	6.300	36.00	0.95	64	7
28	**Lake Camp**	43.36	171.03	674	13.8	17.4	0.490	13.00	0.50	114	12
29	**Lake Roundabout**	43.37	171.05	653	13.9	18.4	0.130	0.74	1.20	63.5	8
30	**Lake Emma**	43.38	171.06	655.5	13.9	24.4	1.550	2.20	2.10	131.5	13
31	**Groynes**	43.27	172.36	25	16.8	21.6	0.018	1.25	2.50	120	6
32	**Lake Forsyth**	43.48	172.44	20	17.0	17.0	5.620	1.60	181.00	30	1
33	**Lake Middleton**	44.16	169.50	526	15.5	19.0	0.230	4.50	0.60	173.5	8
34	**Red Lagoon**	44.18	169.52	589	15.2	19.2	0.160	1.25	0.15	150	21
35	**Swan Lagoon**	44.18	169.55	576	15.2	18.9	0.345	1.40	1.50	65	7
36	**Avon**	44.23	169.38	734	14.4	21.3	0.100	1.50	0.60	89	12
37	**Lake Sylvan**	44.42	168.19	383	14.3	17.4	0.720	19.15	0.50	88	18
38	**Lake Harris**	44.43	168.10	1231	9.6	8.9	0.250	40.00	0.15	112	19
39	**Lake Mackenzie**	44.45	168.10	885.5	11.4	9.2	0.200	34.20	0.15	156.5	14
40	**Gertrude Saddle**	44.44	168.01	1371.5	8.4	6.6	0.010	2.90	0.15	199	19
41	**Lake Howden**	44.49	168.08	684	12.4	12.0	0.100	9.40	0.20	255.5	19
42	**Lake Hayes**	44.58	168.48	329	15.8	19.1	2.030	31.00	1.99	50	12
43	**Lake Johnson**	45.00	168.43	406	15.4	21.0	0.200	28.30	0.40	27	7
44	**"Sugarbowl Tarn"**	45.03	168.49	1799.5	8.2	13.8	0.014	6.15	0.20	195	5
45	**Lake Alta**	45.04	168.48	1882	8.2	8.2	0.130	36.10	0.15	72.5	5
46	**Lake Mistletoe**	45.12	167.49	207	14.6	16.5	0.100	13.65	1.10	52.5	18
	Max	45.12	176.53	1882	18.1	29.4	79.780	40.00	181.00	534.0	21.0
	Min	38.01	167.49	20	8.2	6.6	0.010	0.74	0.15	17.0	1.0
	Mean	42.63	171.56	665	14.1	17.3	2.686	13.65	8.54	132.2	10.7
	Median	43.04	172.14	583.5	14.6	17.5	0.180	10.20	1.11	99.5	9.5
	SD	1.94	2.48	532.3	2.9	4.4	11.780	12.55	27.40	105.5	4.7

chemistry of water samples from each lake is presented in **Table 4.1**. A full list of all measurements and variables is given in **Table B1**, **B2**, and **B3** in **Appendix B**. Sediment cores were taken using a Glew Mini Corer (Glew, 1991) at the deepest point in each lake. Where the main basin was large, or there was more than one sub-basin, several sites were sampled and the samples combined later to form a composite sample. The top 2 cm of each core were extruded while still in the boat, sampled at 1 cm intervals and placed in Whirl-paks®. Sediment samples were kept cool and out of direct sunlight until they could be processed. For a description of the processing methods for chironomid analysis of the surface sediment samples see **Section 3.24** in **Chapter 3**.

When live chironomids were observed in the surface sediments, these were immediately transferred into 95% ethanol for later examination. Surface sweep samples and littoral sediment samples were taken using a D-frame sweep net (363 μm mesh) (Batzer, 2001) for exuviae and live larvae. The contents of the net was transferred to 95% ethanol and picked for chironomid larvae and exuviae in the laboratory under a dissecting microscope. All remains of live larvae and exuviae were mounted in on glass slides in a drop of polyvinyl lactophenol and covered with a glass coverslip. The exuviae and larval remains were examined in order to provide insights into the taxonomy of problem taxa (e.g. *Chironomus* spp. and the Macropelopini). A discussion of these observations is provided in **Chapter 2**.

Even though measurements for surface water temperature were taken in the field, the February mean (hereafter referred to as Feb Mean) (late austral summer) and July (the coldest month) mean minimum air temperatures (hereafter referred to as mean minimum winter temperature (MMWT)) were used as the temperature variables in all numerical analyses. Chironomid assemblages are likely to be influenced by both air temperature (e.g. during pupation, flight, reproduction and dispersal (Hoffman 1986; Walker and Mathewes 1989b)) and water temperature (e.g., larval development rates and mortality effects (Robb 1966)). Walker et al. (1991) and Olander et al. (1997) have demonstrated that there is a close relationship between air and water temperature for shallow polymictic lakes. Therefore, in the absence of long-term water temperature measurements, the use of mean monthly climate data is appropriate. Feb Mean and MMWT temperature measurements were extracted from a climate surface fitted to data from 346 weather stations covering a period of 30 years (Leathwick et al., 1998).

Topographic maps, air photographs and field observations were used to estimate the catchment vegetation, land use, and lake surface area. The surface of the catchment was classified by the relative abundance of 12 variables (**Table B4**, **Appendix B**). The indigenous vegetation was divided into three categories. "Native forest" included all stands of native canopy trees (e.g. *Nothofagus*,

Podocarpus), while "Tussock/grassland" and "Tussock/herbfield" were used to distinguish between montane tussock-land (e.g. *Poa*) and sub-alpine/alpine flora (e.g. *Chionochloa*, Asteraceae, Gentianaceae,
and Ranunculaceae) respectively. "Exotic" refers mainly to stands of exotic timber taxa (e.g. *Pinus*), while "Pasture" refers to areas of land that have been cleared for grazing and are now mainly covered by introduced pasture grasses (e.g. *Pennisetum clandestinum*). "Scrub" refers to smaller indigenous trees and shrubs (e.g. *Discaria toumatou*, *Coprosma*, and *Leptospermum*).
The catchment area occupied by lakes ("Lakes"), swamps ("Swamps"), snow and ice ("Snow"), exposed rock ("Rock/scree"), populated areas ("Populated") and crops ("Crops"; cereals, vegetables etc.) was also defined. The latitude (Lat) and longitude (Long) was taken from hand-held global positioning system (GPS) readings taken in the field.

4.4 STATISTICAL METHODS

4.4.1 Data transformations and screening of samples

All lakes were removed from the original dataset if they produced less than 50 chironomid head-capsules. Quinlan and Smol (2001) argue that a minimum count of 40-50 head-capsules is sufficient for use in inference models where diversity is low. Rarefaction analysis of the species data (Birks and Line, 1992) was used to simulate the effect of count size on taxonomic richness. Rarefaction analysis models the effect of count size on assemblages with varying taxonomic richness. It would be expected that small counts from species rich assemblages would seriously underestimate the actual species richness. Small counts from assemblages that actually contain a small number of species are quite likely to reflect the true taxonomic richness. The computer programme RAREPOLL (Birks and Line, 1992) was used to perform the rarefaction analysis.

Secchi depth measurements were removed from the original environmental dataset as the secchi depth was potentially greater than the lake depth (i.e. the disc was visible on the bottom) in six lakes (**Table 4.1**). Altitude and lake area values were also removed from the environmental dataset. These parameters indirectly affect chironomid distribution (i.e., they affect such factors as temperature and productivity) but are unlikely to have a direct effect on chironomid distribution.

The remaining 33 environmental variables were tested for normality using SPSS® statistical software (SPSS Inc., 2002). Log_{10} transformations were required to normalise all environmental data

except for depth, Lat, Long, Feb Mean, MMWT, pH, and the catchment information. Percentage cover for the various catchment characteristics was square root transformed. Chironomid species data were used in the form of square root transformed percentage data (%). Species were only included in the analyses if they occurred in an abundance of ≥ 2 % in at least 2 lakes.

4.4.2 Exploratory data analysis

Constrained and unconstrained ordinations were performed using CANOCO version 4.5 (ter Braak and Šmilauer, 2002) to explore the relationships between modern chironomid assemblages and environmental variables and catchment characteristics and water chemistry. Rare species were down-weighted in all analyses. Constrained ordination techniques were also used to investigate the effect of environment on species diversity and taxonomic richness. Species diversity was represented by the Shannon Weaver Index (H'). H' was calculated using the equation: $H' = - \sum P_i \ln P_i$, where P_i represents the proportion of the *i*th taxon in the sample (Begon et al., 1986).

Detrended correspondence analysis (DCA)) was used to explore the patterns of compositional variation and biological species turnover (the gradient length). The gradient length provides a guide as to which set of constrained ordination techniques would be most suitable to test the species/environment relationships. Gradient-length values < 2 SD suggest the use of linear methods (e.g. redundancy analysis RDA), while those > 4 SD suggest the use of unimodal methods (e.g. canonical correspondence analysis CCA) (ter Braak, 1995). A DCA also plots chironomid species and sites so as to maximise the variance represented in each DCA axis, without constraining species and sites to the environmental variables. Two artificial "environmental gradients" are created by the DCA algorithm so as to maximise the species variance along each of these "gradients" or DCA axes. Passively fitting the measured environmental variables to a DCA plot provides an indication of whether the variation of the measured environmental variables (the real environmental gradients) are related to the artificial "environmental gradients" created in the DCA.

The unique explanatory power of each significant environmental variable for the total variance in the chironomid species data was tested using a series of partial, constrained ordinations (RDA or CCA) with all other significant environmental parameters as co-variables. Only environmental parameters that retained their significance after these analyses were considered for transfer function development. A check was also performed for outliers by means of the leverage diagnostic in CANOCO 4.5 (ter braak and Šmilauer, 2002). A measure of leverage provides an indication of how extreme the position of a particular sample is in environmental space. As direct gradient analysis

(canonical regression) is an extension of multiple regression, samples with extreme values have a disproportionate effect on the final results. The inclusion of such outliers can give a false impression of the strength and significance of the relationship between to variables (e.g. species and environment) (Golberg and Cho, 2004). The significance of each environmental variable by itself and with co-variables was also tested with a series of partial CCAs after all outliers were removed. Only variables that remained significant after all of the outliers were removed were considered for the development of transfer functions.

The statistical significance of the relationship between environment and species variance for each individual environmental variable was tested by Monte Carlo permutation test (999 unrestricted permutations under the full model). Variables with a significant ($P \leq 0.01$) were retained for further analyses. A cut-off threshold of $P = 0.01$ was set for all significance tests. When a resampling (bootstrap or permutation) method is used with only one test, the adjusted P value is the bootstrap or permutation P value for that test, with no adjustment for multiplicity (Westfall and Soper, 1994). The standard cut-off for considering a test statistic to be statistically different is usually $P < 0.05$. For a single comparison, this indicates that the observed differences would occur by chance only 5% of the time. When multiple comparisons are being made within an experiment, however, the probability of observing a sizable difference for one of the comparisons increases with the number of comparisons being made. This increases the chance of rejection of a true null hypothesis (the species are unrelated to the environmental data), and is called a type I error (Benjamini & Hochberg, 1995).

A minimum number of environmental variables was also sought to act as constraining variables in the final CCA. A minimum number of environmental variables should be sought that explain a similar amount of the total taxonomic variance to the full set of environmental variables. Large reductions in explanatory power and significance (P) of a variable when the effects of other variables are partialled out indicate that this variable is redundant. Environmental variables were immediately removed if their explanatory power and significance was drastically reduced by partialling out all other significant environmental variables in a series of partial CCAs, i.e. if P was greater than 0.1. These variables were therefore entered as supplementary environmental variables in all future constrained ordinations. Environmental variables were automatically included as constraining variables if they were significant to the $P < 0.01$ threshold after the effect of all other environmental variables were partialled out. Environmental variables with P –values ranging between 0.01 and 0.1 were included as constraining variables if they had significant canonical coefficients (as measured by t-values) for the first three axes.

4.4.3 Subdivision of the training set

The training set was divided into sub-sets to enable the testing of co-linearity in the environmental variables (e.g. ionic data and conductivity) and with the specific purpose of developing transfer functions for temperature and lake productivity/chemistry. Firstly the methodology used to detect co-linearity in the environmental variables will be discussed. Secondly the screening methods will be discussed that were used to eliminate lakes for the production of specific transfer-functions. Then the merits of performing screening methods will be discussed as the 'tailoring' of training sets for specific transfer functions involves various assumptions.

A. The "ion data set": a check for co-linearity in the limnological variables:

The training set was initially divided into two sub-sets for the initial analyses depending on the availability of the environmental data. The first sub-set (hereafter referred to as the ion data set) contained 33 lakes. Data pertaining to 33 environmental parameters (depth, Lat, Long , Feb Mean, MMWT, Cond, pH, NO_x-N, RP, TN, TP, Chla, TC, DIC, DOC, Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, SO_4^{2-}, and catchment variables) were available for this dataset (**Appendix B**). A series of constrained ordinations were used to test whether the addition of the 9 water chemistry variables (TC, DIC, DOC, Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, and SO_4^{2}) provided any unique solutions that could not be provided by the 10 limnological variables (depth, Feb Mean, MMWT, Cond, pH, NO_x-N, RP, TN, TP, Chla) that were available for all 46 lakes.

Variance inflation factors (VIFs) produced in CANOCO 4.5 from a canonical correspondence analysis (CCA) were used to identify variables with a high degree of correlation with other environmental variables in the dataset. If the VIF is large (i.e. >20), then the variable is almost perfectly correlated with other variables in the dataset and therefore has no unique contribution to the regression equation (ter braak and Šmilauer, 2002). Variables were removed one at a time until all VIFs were lower than 20. The variable with the highest VIF was removed first. The CCA was re-run until all VIFs were below 20. TC and Cond were removed before the VIFs were examined. Electrical conductivity (Cond) is known to be closely proportional to concentrations of the eight major ions (the *salinity*) Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, CO_3^{-2}, HCO_3^{-}, SO_4^{2-} , and Cl^{-} (Juday and Birge, 1933; Rodhe, 1949). This was confirmed for this dataset with a scatterplot of salinity vs conductivity (**Fig. 4.3**). The concentrations of Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, DIC (CO_3^{-2} and HCO_3^{-}), SO_4^{2-}, and Cl^{-} were

included in the total for the dissolved ionic content (salinity). The correlation coefficient (r^2) was reduced from 0.97 to 0.87 by two outliers, Lake Mackenzie and "Gertrude Saddle" (M and G respectively in **Fig 4.3**). Both of these lakes are located in catchments that contain hornblende-biotite diorite (Wood, 1962). Because these lakes fall well below the trend-line, there are obviously ions contributing to the total salinity in the water from these lakes that were not measured. It is highly likely that Fe^{2+}, Fe^{3+}, Mn^{2+}, and Mn^{4+} concentrations will be significant in these lakes. Troester (1998) found these ions in significant concentrations in groundwater in a diorite bedrock catchment in Puerto Rico.

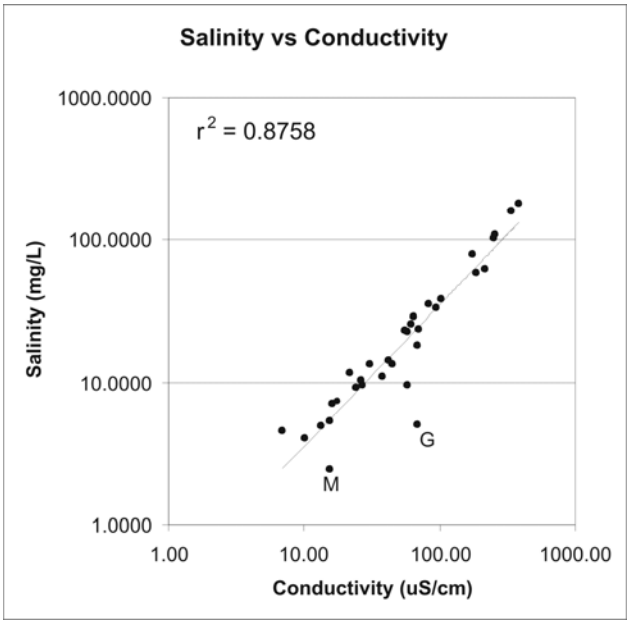


Fig. 4.3: The relationship between salinity (concentration of dissolved solids) and conductivity in the ion training set (n = 33). A trendline is shown and the corresponding correlation coefficient (r^2). Two outliers, Lake Mackenzie (M) and "Gertrude Saddle" (G) reduce the r^2 from 0.97 to 0.87.

TC was also removed before the VIFs were examined as it is the product of IOC and OC.

Partial constrained ordinations (RDA or CCA) were used to check the explanatory power of the remaining environmental variables.

B. The "non-ion data set":

The second group of analyses (hereafter referred to as the non-ion data set) was performed using a data set containing all 46 lakes. This group of analyses tested the explanatory power of the 24 environmental variables (depth, Lat, Long, Feb Mean, MMWT, Cond, pH, NOx, RP, TN, TP, Chla and the 12 catchment variables) available for all of the lakes (**Table B1** and **B2**, **Appendix B**). The catchment variables (catchment vegetation and land-use) were included in these analyses to

investigate whether the catchment data provided any unique information. The chironomids are aquatic, and therefore any effect from the catchment variables is likely to secondary, e.g. through increased nutrient input in farmed catchments. It is possible that certain effects of the catchment variables have not been captured in the measured limnological variables (water chemistry). Human disturbance in the catchment may alter sediment influx, and various chemicals associated with human activity that could effect chironomid distribution may not have been measured (e.g. heavy metals and pesticides). In this case, partial CCAs were used to determine the unique explanatory power of all of the environmental variables. VIFs were examined in a preliminary CCA to check for redundant environmental variables. Variables were also checked using partial constrained ordinations (CCAs or RDAs). It was predicted that temperature would produce a high VIF in this initial CCA. This is to be expected as catchment vegetation itself will be dependent on temperature, lake productivity (TP, TN, Chla) also tends to decrease with increasing altitude (Riera et al., 2000), and most human activity (forestry, agriculture etc.) is at lower altitudes.

Exploratory data analysis of a training set with long gradients for several environmental variables provides a good initial test of which environmental variables are influencing the distribution of New Zealand chironomid taxa. This 43 lake training set was also divided into two sub-sets. All disturbed sites were removed from the training set used to develop the temperature transfer function. The temperature gradient was limited by removal of high altitude lakes for the purpose of developing a transfer function for productivity/chemistry of New Zealand lowland lakes.

C. Tailoring the training set for production of specific transfer functions:

Temperature transfer function

Larocque et al. (2001) argue that quantitative paleoecological reconstructions of Holocene climate change are likely to be most reliable if the modern training sets are developed in regions were the amount of anthropogenic disturbance is minimal. Human activities such as agriculture and forestry can result in extreme nutrient inputs. Because most intensive farming in New Zealand occurs in lowland areas, the elevated nutrient levels in lakes in disturbed lowland catchments could impair our ability to quantify chironomid-climate relationships. Previous studies of this type elsewhere in the world have found that there is a natural trend towards more productive lakes in undisturbed lowland catchments (e.g. Lotter et al., 2001). As productivity and temperature co-vary, it can sometimes be difficult to tell if chironomids are responding to temperature or productivity or both. Disentangling

the effect of nutrients and temperature on chironomid assemblages has proven controversial in the past (e.g. Walker and Mathewes 1987; Warner and Hann 1987). The inclusion of eutrophic and/or hypertrophic lowland lakes is likely to compound this problem.

I therefore performed analyses on a 31 lake subset of the chironomid training set with all of the lakes that were situated in disturbed catchments removed. These lakes plot to the left of the PCA biplot of catchment characteristics and limnological variables (**Fig. 5.2** in **Chapter 5**). Lakes were identified as "disturbed" if the lake catchment contained high percentages of pasture ("Past."), crops ("Crops"), exotic plantation forestry ("Exotic") or populated areas ("Popul."). These lakes are typically eutrophic to hypertrophic.

A temperature transfer function produced from this dataset would be unreliable if it was applied to a lake that experienced natural eutrophic conditions in the past. Highly eutrophic conditions are also possible in the absence of human impact (e.g. Brüchmann and Jörg 2004). Several studies have recently emerged where "tailored" training sets have been used to develop transfer functions for specific environmental variables (e.g. to reconstruct total phosphorus (TP) (Hausmann and Kienast, 2006). These "tailored" transfer functions are produced by removing the effects of all other environmental variables (e.g. pH, conductivity, etc.).

The danger in this approach is that just because the effect of these variables has been removed from the modern dataset, does not mean that these effects will be absent in the fossil record. I believe in the case of the temperature transfer function we would be more likely to find good modern analogues for our fossil assemblages if we remove our lowland lakes in disturbed catchments. However I also believe that it would be good practice to test down-core assemblages with a modern training set that covers reasonable gradients for all environmental parameters that may influence the targeted biological proxy. A CCA (canonical correspondence analysis) biplot of modern and fossil assemblages with significant environmental variables would be useful for this purpose. It would be possible to see if species assemblages are moving in a transect that is parallel to the environmental gradient of interest (**Fig 4.4**). A further test of whether a "tailored" transfer function is reliable would be to examine the similarity (via similarity indexes) between the modern and fossil species assemblages.

Water chemistry or production of New Zealand lowland lakes

Initial exploratory analyses revealed that temperature still explained a large significant amount of the chironomid taxonomic variance, even in the presence of highly eutrophic lowland lakes. Consequently, another 31 lake subset was examined with the intention of developing a transfer

function for lake nutrients/production (TP, TN, or chlorophyll *a*) or conductivity. For this purpose, all lakes with a February mean less than 12 ºC were removed from the dataset (**Fig 4.5**). Once again the issue of variation in the screened environmental variable (in this case temperature) in the fossil record arises. The CCA biplot approach would once again be useful to test the fossil assemblages to see if the assemblages are moving in a CCA bi-plot space trajectory that is parallel to the environmental gradient of interest. The main purpose of the production/chemistry transfer function will be to investigate human impact on New Zealand lakes, and to establish pre-impact states to serve as a target for restoration. Detailed climate records for most of New Zealand extend back to ca. 1860 (Salinger, 1998). These climate records show temperature fluctuations that are no greater than 2 ºC for this time period (**Fig 4.6**). Longer term climate records from tree-rings (Xiong and Palmer, 2004) (**Fig. 4.7**) show a slightly larger degree of variation when the record is extended back to 1720, which is well before the settlement of Europeans in New Zealand and the initiation of pastoral farming. If temperature does not show a significant relationship to the species variance in the screened nutrients/production/conductivity training set (with a temperature gradient of 6 ºC) and a robust transfer function is developed for nutrients, production or conductivity, the minimal ammount of temperature variation over the last 270 years would make it highly likely that changes in fossil chironomid assemblage do actually correspond to changes in lake water chemistry. Intra set correlation co-efficients produced using a CCA including all significant environmental variables were checked to investigate the co-linearity of these environmental variables in the reduced datasets.

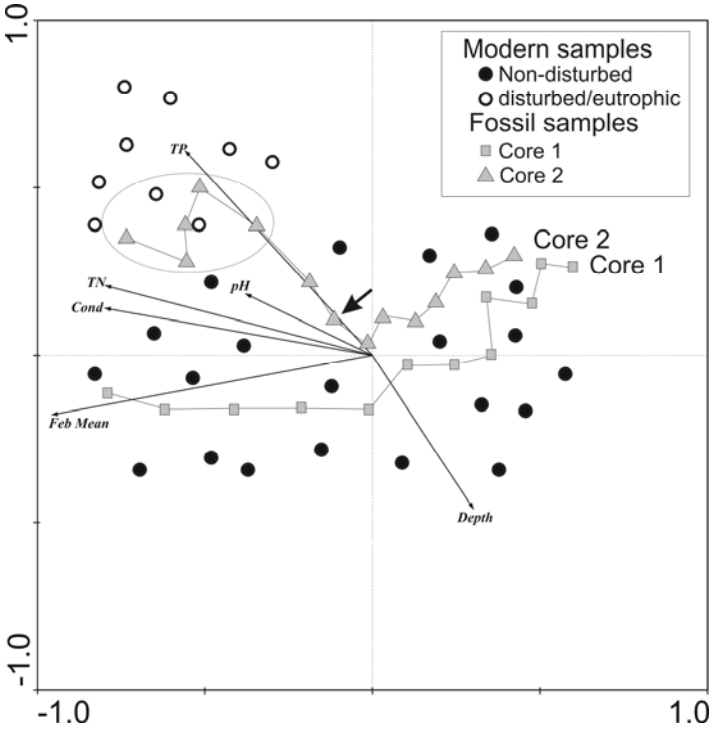


Fig 4.4: A hypothetical CCA biplot of modern chironomid samples constrained to significant ($P < 0.01$) environmental variables and assemblages (species not shown). Fossil samples have been fitted passively; i.e. they are constrained by species composition but not the environmental parameters. Core 1 is more likely to provide more reliable temperature reconstructions than Core 2. Fossil chironomid assemblages after the arrowed sample in Core 2 are likely to be a product of both temperature (February Mean "Feb Mean") and water chemistry (Conductivity "Cond", Total Nitrogen "TN", Total Phosphorus "TP", and pH. Removal of the eutrophic samples from disturbed catchments would result in poor analogues in Core 2 for the final 5 samples (circled).

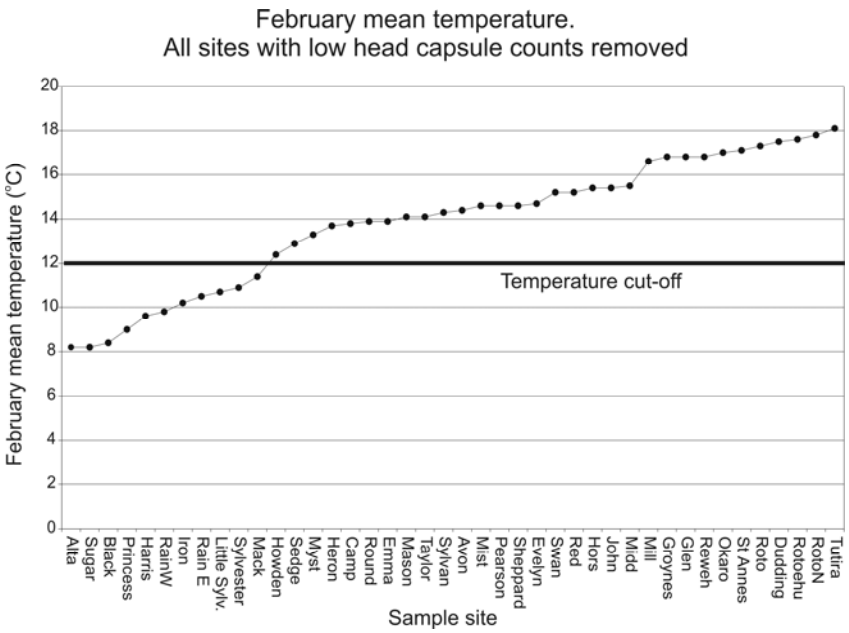


Fig 4.5: February mean temperatures for all of the sites in the modern training set (minus sites with low counts). An arbitrary cut-off of 12ºC was selected to remove the extreme effect of temperature on the production/chemistry training set. This reduces the temperature gradient from 10 to 6ºC.

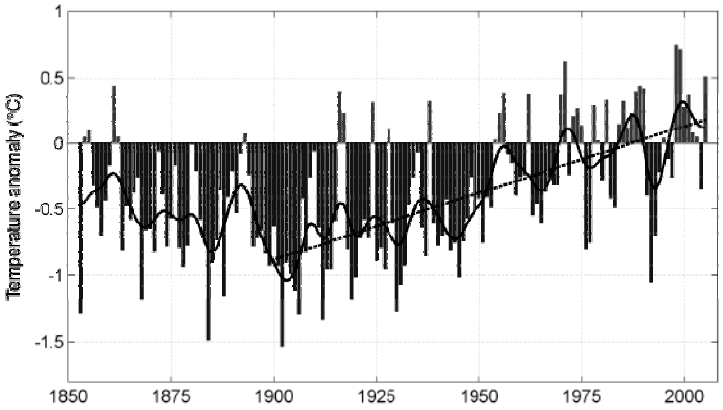


Fig 4.6: Composite temperature record for New Zealand from 1850 to 2005 from www.niwascience.co.nz (based mostly on the published record of Salinger (1998). Darker curved line (smoother) indicates decadal variability. Dashed line is the trend from 1900 to 2005. Smoothed temperature values do not exceed -1ºC deviation from the modern mean, while extreme values reach -1.5ºC deviation from the modern mean.

New Zealand February-March temperature inferred from *Libocedrus* tree rings (Xiong and Palmer, 2004)

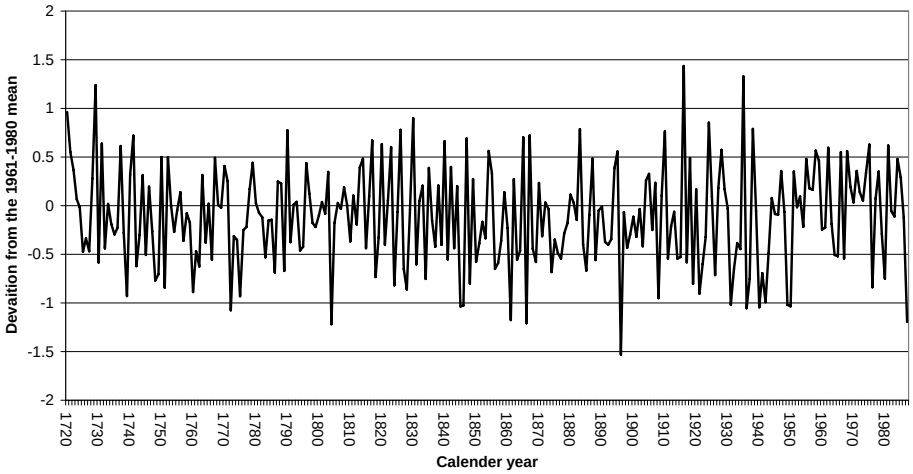


Fig 4.7: Reconstructed February to March temperature extending back to 1720 based on tree rings from *Libocedrus*. Produced from raw data from Xiaong and Palmer (2004) available on the National Oceanic & Atmospheric Administration (NOAA) website. www.ncdc.noaa.gov/paleo/paleo.html.

4.4.4 Model development and assessment

Quantitative transfer functions for the significant environmental variables selected in the CCAs and RDAs were developed in the computer program C2 (Juggins, 2003). Environmental variables that retained a significant relationship ($P \leq 0.01$) to total species variance, had a high explanatory power (λ_1/λ_2) and explained a high percentage of the total species variance were considered for transfer-function development. Gradient lengths for the first axis in a detrended canonical correspondence analysis (DCCA) constrained to a single environmental parameter were used to decide between linear (partial least squares (PLS)) or unimodal (weighted averaging (WA) and weighted averaging-partial least squares (WA-PLS)) models (Birks 1995, 1998). Robust transfer functions were those that had a low root mean squared error of prediction (RMSEP), a high coefficient of determination (r^2_{jack}) and a low mean and maximum bias (Birks, 1998).

Species response curves were also developed and assessed using CANOCO 4.5. A series of different generalized linear models (GLMs) (linear gaussian, quadratic gaussian, quadratic poisson, etc.) were trialled to test which taxa displayed a statistically significant ($P \leq 0.01$) response to the environmental variable in question. Reconstructions based on assemblages dominated by taxa that do not show a significant relationship to the reconstructed variable are likely to be unreliable.

CHAPTER 5: THE DEVELOPMENT OF CHIRONOMID-BASED INFERENCE MODELS FOR PALEOENVIRONMENTAL RECONSTRUCTIONS

PART II: EXPLORATORY DATA ANALYSES. RESULTS & DISCUSSION

5.1 RESULTS

5.1.1 The relationship between catchment type and limnology.

A PCA bi-plot of environmental variables and sample sites is provided in **Fig. 5.1**. Catchment variables (vegetation, etc.) are coloured dark blue, while limnological variables (lake depth, water chemistry, etc.) are coloured red. St Anne's Lagoon (Lake number 19 in **Table 4.1** and **Appendix B**) was removed from the RDA because CANOCO 4.5 identified it as an outlier due to extreme values for TP and Cond. Correlation matrices (inter-set and intra-set) for all environmental variables are provided in **Table C1**, **C2**, and **C3** in **Appendix C**. A summary of the results from the RDA are shown in **Table 5.**1. Abbreviations used in all diagrams are listed in **Table 5.2**.

Axes	1	2	3	4	Total variance
Eigenvalues :	0.306	0.147	0.115	0.077	1
Cumulative percentage variance of species data :	30.6	45.3	56.7	64.4	
Sum of all eigenvalues					1

Table 5.1: Summary results for RDA of the environmental variables from the 43 lake training set in CANOCO 4.5

PCA axis 1 explains most (30.6%) of the variation in the environmental data. This axis is both a temperature (Feb Mean, correlation with axis 1 (corr. ax. 1) = -0.951) and productivity (Chla: corr. ax. 1 = -0.857) gradient. There is also a tendency for lakes plotting to the left of PCA axis 1 to have higher conductivity and higher concentrations of TN (corr. ax. 1= -0.776 and -0.779 respectively). Low altitude lakes plot to the left of PCA axis 1, while high altitude lakes plot to the right of the axis. In terms of catchment characteristics, low altitude sites are subject to more human disturbance, indicated by the increasing influence of pasture ("Past."), exotic trees ("Exotic") and populated areas ("Popul.") to the left of PCA axis 1 (corr. ax. 1= -0.768, -0.640, and -0.271 respectively).

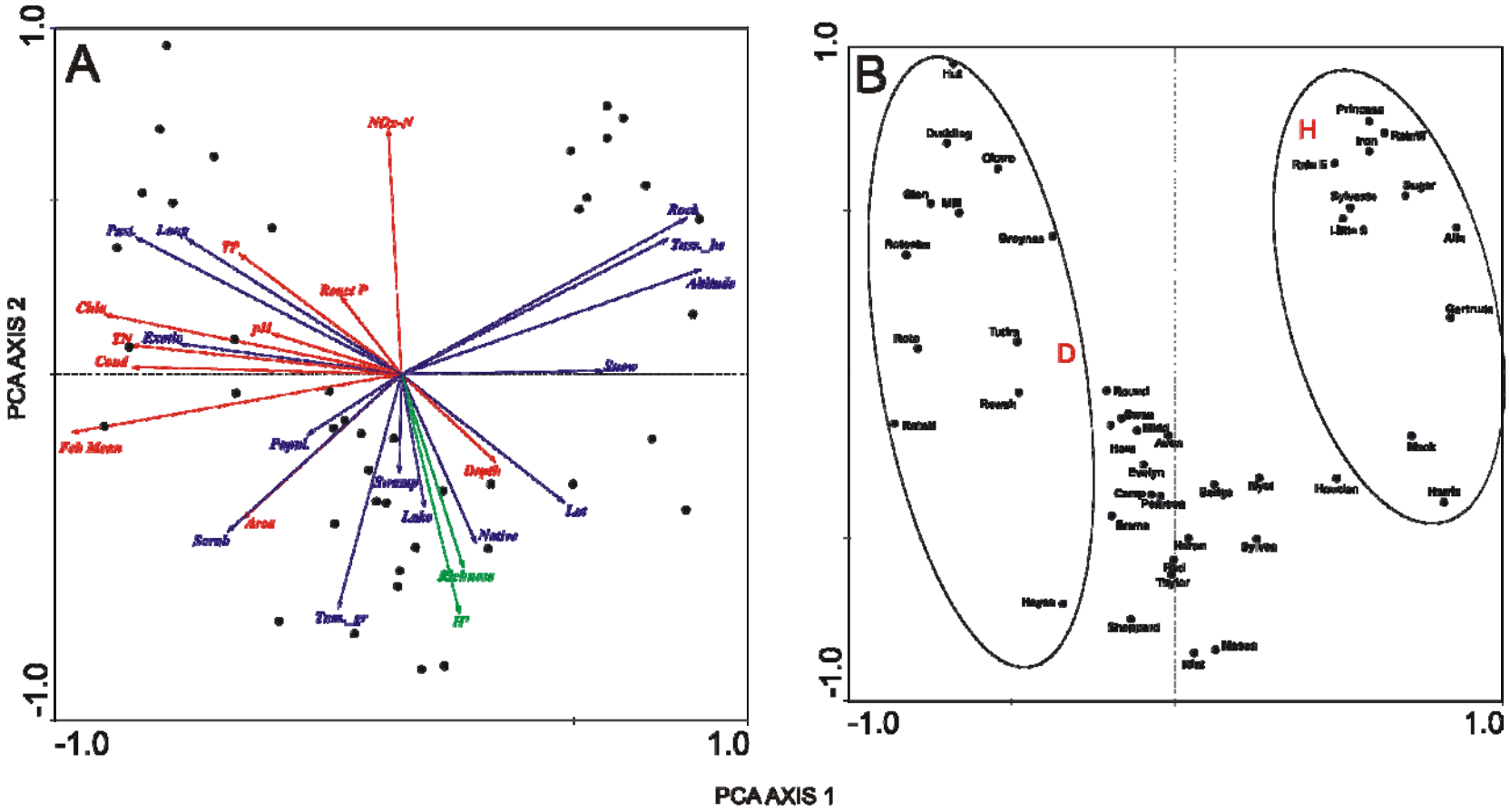


Fig. 5.1: PCA biplot (A) and PCA plot (B) of training set sites and environmental variables. Red arrows correspond to limnological variables (Feb Mean is directly correlated with water temperature. Dark blue arrows correspond to geographic and catchment characteristics. Green arrows correspond to chironomid taxonomic richness and diversity (H') Circled sites in the PCA plot of training set sites: D = disturbed sites removed from the temperature training set. H = high altitude sites removed for the lowland productivity/conductivity training set.

Taxa		Environmental variables		Lakes			
Ablabes.	*Ablabesmyia mala*	Altitude	Altitude of lake	RotoN	Lake Rotorua N	Myst	Mystery Tarn
Chir.spa	*Chironomus* sp. a	Area	Surface area of lake	Rotoehu	Lake Rotoehu	Evelyn	Lake Evelyn
Chiron.s	*Chironomus* spp.	Chla	Chlorophyll *a*	Reweh	Lake Rerewhakaaitu	Heron	Lake Heron
Clad. cur	Cladopelma curtivalva	Cond	Conductivity	Okaro	Lake Okaro	camp	Lake Camp
Corynoc.	*Corynocera* Undescribed sp.	Depth	Depth of sediment sample	Tutira	Lake Tutira	Round	Lake Roundabout
Crict.ac	*Cricotopus aucklandensis*	Exotic	% exotic trees in catchment	Dudding	Lake Dudding	Emma	Lake Emma
Crict zl	*Cricotopus zealandicus*	Feb Mean	February mean air temperature	Iron	Iron Lake	Groynes	Groynes
Macrop.	Tribe Macropelopini	Lake	% lakes in catchment	Sylveste	Lake Sylvester	Fors	Lake Forsyth
Naon.for	*Naonella forsythi*	Lat	Latitude of lake	Little S	Little Sylvester Lake	Midd	Lake Middleton
Naon.kim	*Naonella kimihia*	Long	Longitude of lake	RainW	Rainbow Skifield W	Red	Red Lagoon
Ortho. C	Orthoclad species C	MMWT	Mean minimum winter temperature	Rain E	Rainbow Skifield E	Swan	Swan Lagoon
Para.plu	*Paratrichocladius pluriserialis*	Native	% native forest in catchment	Sedge	Lake Sedgemere	Avon	Avon
Paratan.	*Paratanytarsus grimmii*	NOX-N	Reactive nitogen (NO2, NO3)	Princess	Princess Bath	Sylvan	Lake Sylvan
Paroch.	*Parochlus* spp.	Past.	% pasture in catchment	Roto	Lake Rotorua S	Harris	Lake Harris
Pauci.	*Paucispinigera* sp.	pH		Hors	Horseshoe Lake	Mack	Lake Mackenzie
Polyped.	*Polypedilum* spp.	Popul.	% populated area in catchment	Taylor	Lake Taylor	Gertrude	Gertrude Saddle
Smitt.	*Smittia verna*	React P	Reactive phosphorus	mason	Lake Mason	Howden	Lake Howden
T.fune	*Tanytarsus funebris*	Rock	% bare rock in catchment	Sheppard	Lake Sheppard	Hayes	Lake Hayes
T.vesp	*Tanytarsus vespertinus*	Scrub	% Scrub in catchment	St Annes	St Annes Lagoon	John	Lake Johnson
		Snow	% Snow & ice	Mill	Mill	Sugar	"Sugarbowl Tarn"
		Swamp	% swamp in catchment	Greta	Lake Greta	Alta	Lake Alta
		TN	Total nitrogen	Glen	Glen	Mist	Lake Mistletoe
		TP	Total phosphorus	Hut	Hut		
		Tuss._gr	% Ttussock grassland in catchment	Pearson	Lake Pearson		
		Tuss._he	% Tussock/herbfield				

Table 5.2: Abbreviations used in the tables and diagrams in this thesis.

PCA axis 2 explains 14.7% of the variation in the environmental data. In terms of limnological variables, PCA axis 2 is primarily a nutrient gradient as reactive nitrogen ("NO_X-N"), reactive phosphorus ("React P") and total phosphorus ("TP") are most closely correlated to PCA axis 2 (corr. ax. 2 = 0.708, 0.224, and 0.347 respectively, see Table X.4 in Appendix X). In terms of catchment characteristics, PCA axis 2 primarily distinguishes between the land use and vegetation types of the mid to low altitude sites. Sites located at the bottom of PCA axis 2 are situated in catchments dominated by montane tussock grassland ("Tuss._gr", corr. ax. 2 = -0.676) or native forest ("Native": corr. ax. 2= -0.486). Sites situated towards the top of PCA axis 2 are typically intensively farmed (high percentage of pasture ("Past.").

A correlation matrix produced from a RDA of the catchment and limnological variables is provided in **Table C1** and **C2** in **Appendix C**. The percentage of pastoral farming in the catchment ("Past.") was most closely correlated to productivity (Chla: correlation co-efficient (CC) = 0.723) and electrical conductivity (Cond: CC = 0.684). "Past." was also highly correlated with nutrient concentrations (TP and TN, CC with "Past." = 0.56 and 0.46 respectively). High altitude lakes were located in catchments dominated by rock ("Rock") and tussock and herbfield ("Tuss._he") (CC with altitude = 0.897 and 0.75 respectively). High altitude lakes were typically unproductive with the CC of TN, TP and Chla with altitude equalling -0.615, -0.348 and -0.657 respectively. High altitude water bodies also had low values for electrical conductivity (Cond) with the CC of Cond with respect to altitude equalling -0.747.

5.1.2 Chironomid taxonomic data

Excel spreadsheets containing all the chironomid taxonomic data (raw counts and percentage data) for the 46 lake training set is provided in ***Spreadsheet E3*** *on the supplementary data disc (****Appendix E).***

51 chironomid taxa were identified and enumerated from the 46 lake training set (**Table 5.3**). Only 3 lakes failed to produce sufficient head-capsules (≥ 50; Lakes 21, 32, and 43: see **Table 4.1**). These lakes were excluded from further analyses. Rarefaction analysis revealed that the mean sample size (132 head-capsules) captured an average of 80% of the actual taxonomic richness in the New Zealand chironomid assemblages (**Fig. 5.2b**). A regression of taxonomic richness versus total head-capsule count (**Fig. 5.2a**) revealed a low correlation ($r^2 = 0.2253$) between the sample size and taxonomic richness. A table with the output results from RAREPOLL (Birks and Line, 1992) is

provided in **Spreadsheet E4** in **Appendix E**. Eight chironomid taxa were the most common (number of non zero occurrences (N)) and the most abundant (mean number of occurrences (Mean) (**Table 5.3**). These were the *Chironomus* spp. morphotype, head-capsules belonging to the tribe Macropelopini, *Corynocera* sp., *Naonella kimihia*, *Cricotopus aucklandensis*, *Polypedilum* spp., *Tanytarsus funebris* and *Tanytarsus vespertinus* (in order of decreasing mean abundance). Only 19 taxa occurred at abundances of ≥ 2% in at least 2 lakes; *Ablabesmyia mala*, *Cladopelma curtivalva*, *Cricotopus zealandicus*, *Naonella forsythi*, Orthoclad sp. C, *Paratrichocladius pluriserialis*, *Paratanytarsus grimmii*, *Parochlus* spp., *Paucispinigera* sp., *Smittia verna*, *Chironomus* sp. a, plus the eight most common taxa mentioned above were included in these 19 taxa.

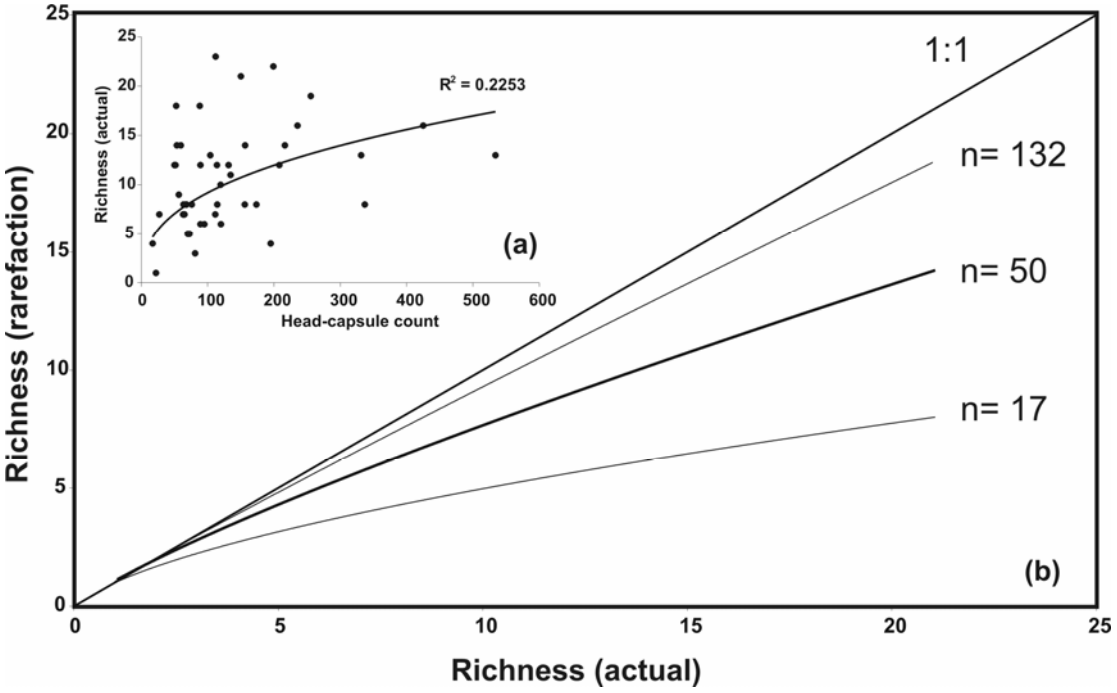


Fig 5.2: Taxon richness in subfossil chironomid samples from New Zealand. **(a)** Relationship between total number of head-capsules and actual sample richness. **(b)** Comparison of richness before and after rarefaction analyses calculated for head-capsule numbers (n) = 17 (lowest count), 50 (accepted minimum count for inclusion of a lake) and 132 (mean number of head-capsules counted for each lake). Rarefaction analysis predicts the taxonomic richness produced by each sample size with respect to the actual taxonomic richness. For example, for the minimum sample size (n = 50) yields 10 taxa (y-axis) for a sample that actually has 14 taxa (x –axis). This equates to ca. 70% of the actual taxonomic richness. The mean sample size (n = 132) performs better with a sample yielding 18 taxa under-predicting the actual taxonomic richness by 2. This equates to 90% of the actual taxonomic richness.

Table 5.3: The 51 chironomid taxa encountered in the surface sediments of the training set.

N= number of non-zero occurrences, N2 = Hill's N2. Most common taxa in bold text.

All taxa occurring at an abundance of ≥2% in at least 2 lakes are marked with an *

No.	Taxon Name	N	Hill's N2	Maximum	Mean
1	*Ablabesmyia mala**	15	8.67	9.35	1.14
2	*Camptocladius* De Geer	3	2.40	1.90	0.08
3	***Chironomus* spp.***	**46**	**30.74**	**100.00**	**36.71**
4	***Cladopelma curtivalva****	24	12.33	18.24	2.55
5	***Corynocera* sp.***	24	13.26	56.90	9.89
6	*Corynoneura*	8	5.31	3.70	0.25
7	*Cricotopus* spp.	12	4.79	6.28	0.34
8	***Cricotopus aucklandensis****	**34**	**12.37**	**56.07**	**5.88**
9	*Cricotopus hollyfordensis*	1	1.00	0.96	0.02
10	*Cricotopus planus*	1	1.00	0.19	0.00
11	*Cricotopus zealandicus**	15	9.56	6.18	0.80
12	*Eukiefferiella brundini*	4	2.75	3.81	0.16
13	*Eukiefferiella insolida*	1	1.00	2.00	0.04
14	*Eukiefferiella* spp.	4	3.28	1.94	0.11
15	*Harrisius pallidus*	2	1.77	1.90	0.06
16	*Hevelius carinatus*	6	3.12	4.02	0.18
17	*Kaniwhaniwhanus chapmani*	2	1.79	2.27	0.07
18	*Kiefferulus opalensis*	1	1.00	11.54	0.25
19	Larsia sp.	1	1.00	1.87	0.04
20	**Macropelopiini***	**37**	**19.53**	**53.85**	**10.06**
21	*Maoridiamesa* Pagast	3	1.34	7.14	0.18
22	***Naonella kimihia****	**33**	**13.24**	**61.38**	**8.75**
23	*Naonella forsythi* *	11	6.57	11.03	1.15
24	*Naonella* "305"	3	1.68	2.68	0.08
25	Orthoclad sp. A	5	3.84	1.90	0.13
26	Orthoclad sp. I	5	3.27	2.94	0.13
27	Orthoclad sp. B	2	1.76	1.94	0.06
28	Orthoclad sp. C*	11	7.81	3.81	0.40
29	Orthoclad sp. G	6	4.29	1.70	0.12
30	Orthoclad sp. 1/6	2	1.95	0.89	0.03
31	Orthoclad sp. J	3	2.76	0.85	0.04
32	Orthoclad sp. D	1	1.00	0.50	0.01
33	Orthoclad sp. E	1	1.00	0.64	0.01
34	*Paratrichocladius pluriserialis**	7	3.61	20.59	1.14
35	*Parachironomus cylindricus*	2	1.62	1.14	0.03
36	*Paratanytarsus grimmii* *	10	5.05	8.55	0.49
37	*Parochlus* spp.*	12	4.07	22.11	1.09
38	*Paucispinigera**	9	5.37	4.70	0.30
39	Pentaneurini	3	2.34	2.59	0.11
40	*Pirara matakiri*	2	1.52	2.68	0.07
41	*Podochlus*	1	1.00	0.50	0.01
42	*Podonomus*	2	1.91	2.01	0.07
43	***Polypedilum* spp.***	**25**	**7.07**	**80.95**	**5.74**
44	*Pseudochironomus*	2	1.81	0.46	0.02
45	*Smittia verna**	6	4.42	3.74	0.24
46	*Stictocladius*	1	1.00	1.87	0.04
47	*Tanytarsus spp.*	14	8.58	3.41	0.38
48	***Tanytarsus funebris****	**30**	**14.30**	**35.78**	**5.34**
49	***Tanytarsus vespertinus****	**24**	**9.91**	**32.14**	**4.22**
50	*Xenochironomus canterburyensis*	3	2.99	0.96	0.06
51	*Chironomus sp. a**	8	5.77	1.00	0.08

5.1.3 Chironomid diversity and taxonomic richness

Values for taxonomic richness (# taxa) and diversity (H') are provided in **Table B3** in **Appendix B**. The number of species per site (in all sites with head-capsule counts greater than 30) ranged from 3 to 21 taxa (**Fig. 5.3B**). Initially, chironomid taxonomic richness ("Richness") was most positively correlated with the percentage of snow and ice in the catchment ("Snow"). A check for outliers using the leverage diagnostic in CANOCO 4.5 identified two lakes (38 and 40) based on this environmental parameter. These two lakes were removed from the dataset. This resulted in the CC for "Snow" and taxonomic richness to drop to 0.02. After removal of these two lakes the percentage of native forest ("Native") was most positively correlated with taxonomic richness (CC = 0.5). Prior to the removal of the two outliers, the CC of "Native" with taxonomic richness was 0.37. Taxonomic richness is most negatively correlated to productivity ("Chla"), and the concentration of reactive nitrogen (NO_X-N) (CCs = -0.31 and -0.27 respectively).

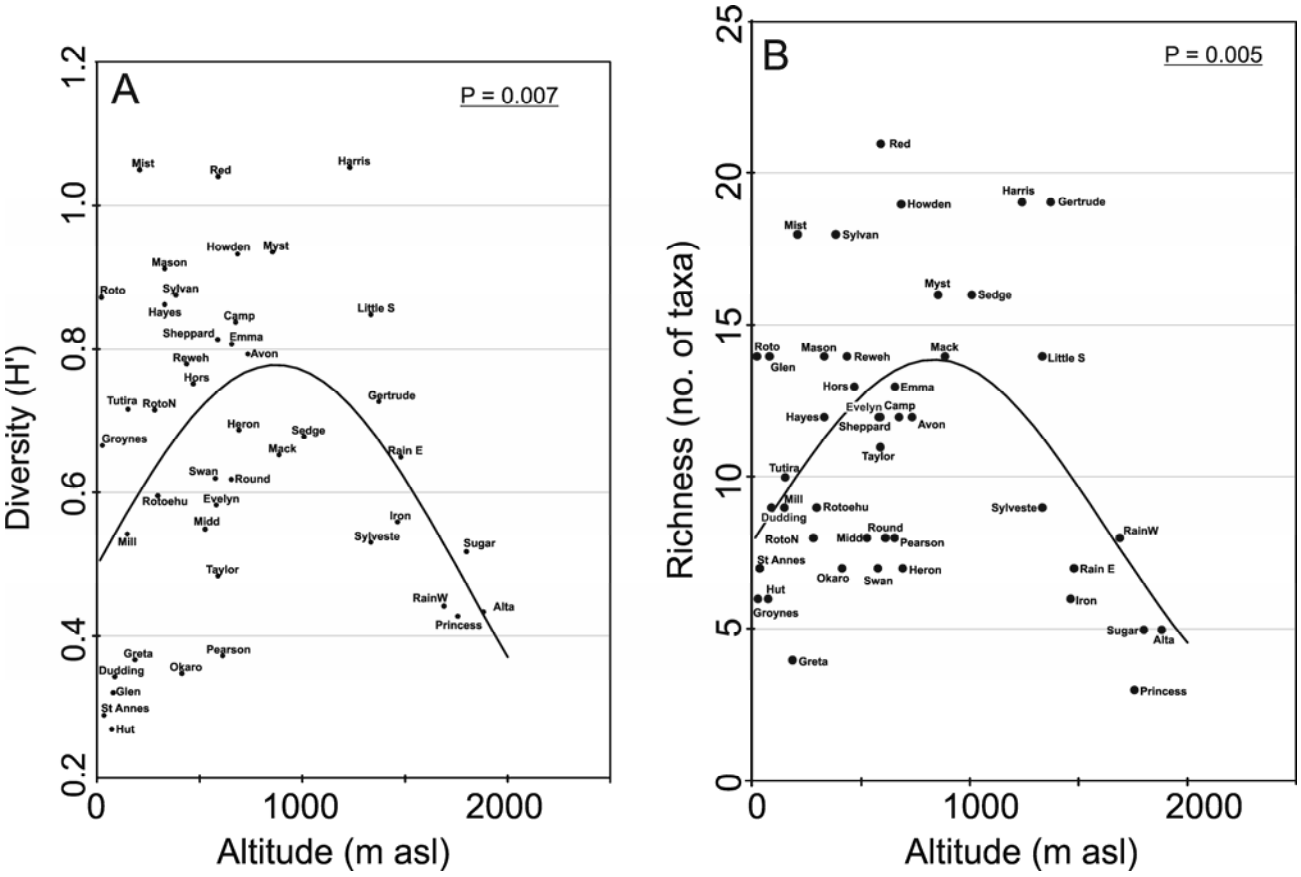


Fig. 5.3: A. Chironomid taxonomic diversity (H') vs altitude with a quadratic poisson GLM fitted. **B.** Taxonomic richness vs altitude with a quadratic poisson GLM fitted. Abbreviations for sites listed in **Table 5.4**.

Values for chironomid taxonomic diversity were typically low, ranging from 0.26 to 1.05 (**Table B3** in **Appendix B** and **Fig. 5.3A)**. chironomid diversity (H') was also positively correlated with the percentage of native forest ("Native") and scrub ("Scrub") (CC = 0.32 for both variables). H' was also positively correlated with the percentage of montane tussock grassland ("Tuss._gr") in the catchment and diversity (CC = 0.3). Diversity was most negatively correlated with the percentage of pastoral farming in the catchment ("Past."), Chla, and NO_X-N (CC = -0.36, -0.34, and -0.35). Diversity was also negatively correlated to longitude ("Long") (CC = -0.35), but this variable was highly correlated to Chla (CC = 0.68) (**Table C1** and **C2** in **Appendix C**).

From the PCA bi-plot it appears that the highest chironomid taxonomic richness and diversity occurs at mid altitude sites. Response curves for diversity and taxonomic richness were tested in CANOCO 4.5. A quadratic poisson model best explained the variation in taxonomic richness and diversity with respect to altitude. The fit of the quadratic poisson model was slightly better with the response of taxonomic richness to altitude (P = 0.005) than it was with diversity (P = 0.007). The fitted curves for diversity and taxonomic richness are provided in **Fig. 5.3A** and **B**. There is a tendency for a low taxonomic richness (<15) at low altitudes with a peak in taxonomic richness at an altitude of around 1000m. Taxonomic richness decreases above 1000m with the lowest taxonomic richness of the entire training set in the high altitude sites.

The low altitude low taxonomic richness assemblages were dominated by head-capsules belonging to *Chironomus* sp. a and *Chironomus* spp.. The high altitude low taxonomic richness assemblages (e.g. Princess Bath and Lake Alta in **Fig. 5.3B**) were dominated by head-capsules belonging to *Chironomus* spp., *Tanytarsus* spp. (both *T. vespertinus* and *T. funebris*) and the tribe Macropelopini. The highest taxonomic richness (21) occurred in Red Lagoon, a shallow oligotrophic lake with low conductivity and a dense coverage of macrophytes over the entire lake bottom. Red Lagoon also had a high taxonomic diversity (1.03). Lake Mistletoe and Lake Harris also had high taxonomic diversities (both ca 1.05). Lake Mistletoe was a shallow (~13m) oligotrophic lake located in West Coast Beech (*Nothofagus* spp.) forest.

Determining the main environmental drivers of New Zealand chironomid taxonomic variance:

The following sections are concerned with determining which environmental variables are the main drivers of taxonomic variance in the New Zealand chironomids. The flow chart provided in ***Fig. 5.4*** *is a summary of the screening process that was necessary to eliminate the confounding effects of temperature and nutrients in this training set. Four main series of analyses were performed; these are shown in four main columns in* ***Fig. 5.4****. The flow chart indicates which lakes and environmental variables were removed, and why they were removed. A summary statement is provided at the bottom of each column, outlining the interpretation of each of the four groups of analyses including which variables are most suitable for transfer- function development.*

5.1.4 Co-linearity of the environmental variables in the ion datset

A DCA of the taxonomic data from the ion dataset revealed that the species turnover (the gradient length) was 2.3 (**Table C4**, **Appendix C**). This lies above the suggested cut-off for linear ordination methods (2 SD) and below the suggested cut-off for unimodal methods (4 SD) (ter Braak, 1995). Therefore initial outputs from a RDA and CCA were checked to see which method was more appropriate. An initial RDA revealed that this method captured a greater proportion of the total species variance (58%) when all environmental variables were included. However, neither axes were significant ($P < 0.05$) after the initial RDA, and the selective removal of sites identified as outliers using the leverage diagnostic reduced the significance of both axes even further. A CCA explained slightly less of the total species variance (39%), but both axes were significant (P=0.001). Therefore CCA was selected as the preferred method in this case.

An initial CCA of the ion datset and the chironomid taxonomic data from the smaller 33 lake dataset revealed extreme variance inflation factors (VIFs) for the ionic data (**Table C5**, **Appendix C**). OC and Mg^{2+} were removed because they had VIFs higher than 20 (25 and 24 respectively). Na^{+} was also removed as it has a high VIF (17) compared to the other remaining environmental variables. The remaining 14 environmental variables were checked individually for significance with partial CCAs (**Table 5.4**). Feb Mean, IOC, K^{+}, Ca^{2+}, SO_4^{2-}, TN, and Chla had significant

Variable	λ_1/λ_2	P	Cum %	Outliers
Area	0.116	0.666	2.70	Emma, Sylvan
Feb Mean	0.706	0.001	15..1	
pH	0.165	0.335	4.10	Roto, Gertrude
Depth	0.113	0.661	2.60	
IOC	0.419	0.006	9.40	Black, Mack, Myst
K	0.817	0.001	15.90	
Ca	0.667	0.001	10.70	Gertrude, Mack
Cl	0.352	0.027	7.90	Princess, Glen, St Annes
SO4	0.464	0.002	9.30	Glen, Mill,
NOx-N	0.116	0.720	2.50	Hut
React P	0.218	0.242	4.40	St Annes, Hut,
TN	0.696	0.001	13.60	Mack
TP	0.271	0.091	5.60	St Annes, Hut, Roto,
Chla	0.571	0.001	11.40	Glen, Roto, Mill

Table 5.4: Summary results from a series of CCAs of the chironomid taxonomic data constrained to the environmental variables remaining after those with high VIFs were removed. Numbers in the "Outliers" column refer to lakes in Table 4.1 (p. 67). Variables that did not have a significant relationship to species variance ($P \leq 0.01$) are highlighted with grey.

relationships to the total chironomid species variance (**Table 5.4**). A series of partial CCAs with the effects of all the other environmental parameters partialled out revealed that temperature (Feb Mean) was the only variable with a unique, significant explanatory power for chironomid species variance in the ion datset (**Table C3**, **Appendix C**). The explanatory power (λ_1/λ_2), and significance (P) of all environmental variables was dramatically reduced by partialling out the effect of Chla. The explanatory power and significance of all environmental variables except for K^+ was dramatically reduced by partialling out the effect of temperature (Feb Mean)

Because the ion dataset did not produce any unique solutions, all further analyses focused on the remaining 43 lakes from the "non-ion dataset" for which 21 environmental variables were available.

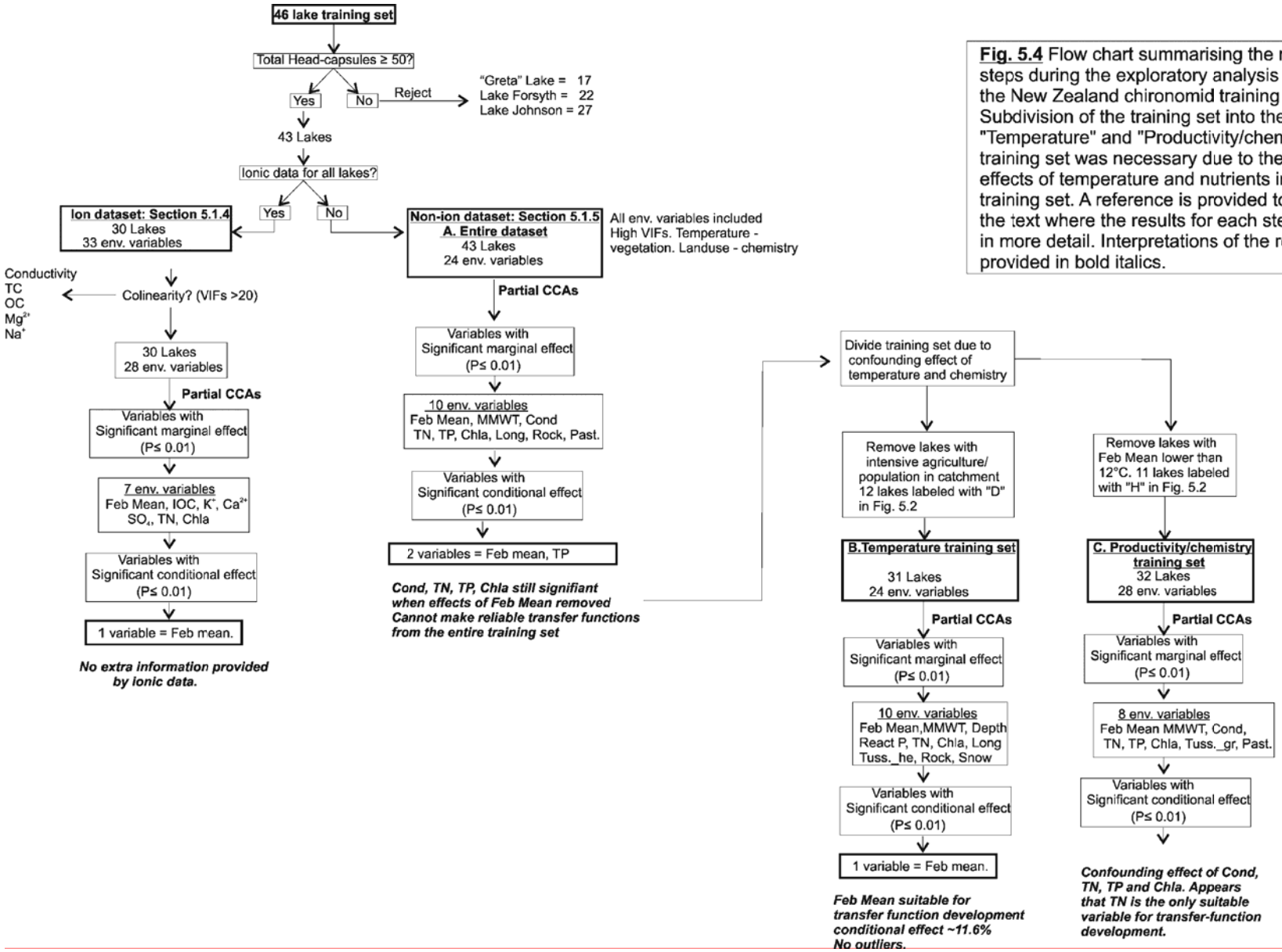


Fig. 5.4 Flow chart summarising the main steps during the exploratory analysis of the New Zealand chironomid training set. Subdivision of the training set into the "Temperature" and "Productivity/chemistry" training set was necessary due to the confounding effects of temperature and nutrients in the entire training set. A reference is provided to the section in the text where the results for each step are provided in more detail. Interpretations of the results are provided in bold italics.

5.1.5 Exploratory analysis of the "non- ion" dataset

A. Entire dataset:

Unconstrained ordinations:

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.324	0.141	0.101	0.066	1.449
Lengths of gradient :	2.583	2.242	1.759	1.479	
Cumulative percentage variance of species data :	22.3	32.1	39.1	43.6	
Sum of all eigenvalues					1.449

Table 5.5: Results of a detrended correspondence analysis (DCA) of the chironomid taxonomic data from the entire training set.

The first DCA axis captured 22.3% of the total variation in the chironomid species data, while the second DCA axis captured 9.8% (**Table 5.5**). DCA plots are depicted in **Fig. 5.5**. Sites plotting to the left of DCA axis 1 typically had high abundances of *Tanytarsus vespertinus*, *Ablabesmyia mala*, *Naonella forsythi*, *Smittia verna*, Orthoclad sp. C, *Parochlus* sp. and *Paucispinigera* sp.. Sites plotting to the right of DCA axis 1 typically had high abundances of *Chironomus* sp. a, *Paratrichocladius pluriserialis* and *Polypedilum* spp.. Sites plotting at the bottom of DCA axis 2 had high abundances of *Corynocera* sp., while those plotting at the top of DCA axis 2 had high abundances of *Paratanytarsus grimmii*, *T. vespertinus*, *Ablabesmyia mala*, *T. funebris*, and *Naonella kimihia*. All environmental variables were fitted passively to a DCA plot of the lake sites based on chironomid assemblages (**Fig. 5.5C**). DCA axis 1 is primarily an altitudinal gradient, with high altitude sites plotting to the left and low altitude sites plotting to the right. February mean temperature (Feb Mean) is the variable with the highest correlation with DCA axis 1 (correlation with DCA axis 1 = 0.81), followed by the percentage of pasture in the catchment ("Past."), Chla, TN, and Cond (correlation with DCA axis 1 = 0.761, 0.719, 0.687, and 0.661 respectively). The catchment characteristics "Swamp", "Scrub", "Native", and "Exotic" are most highly correlated with DCA axis 2 (correlation with DCA axis 2 = -0.331, 0.233, -0.159, and 0.185 respectively).

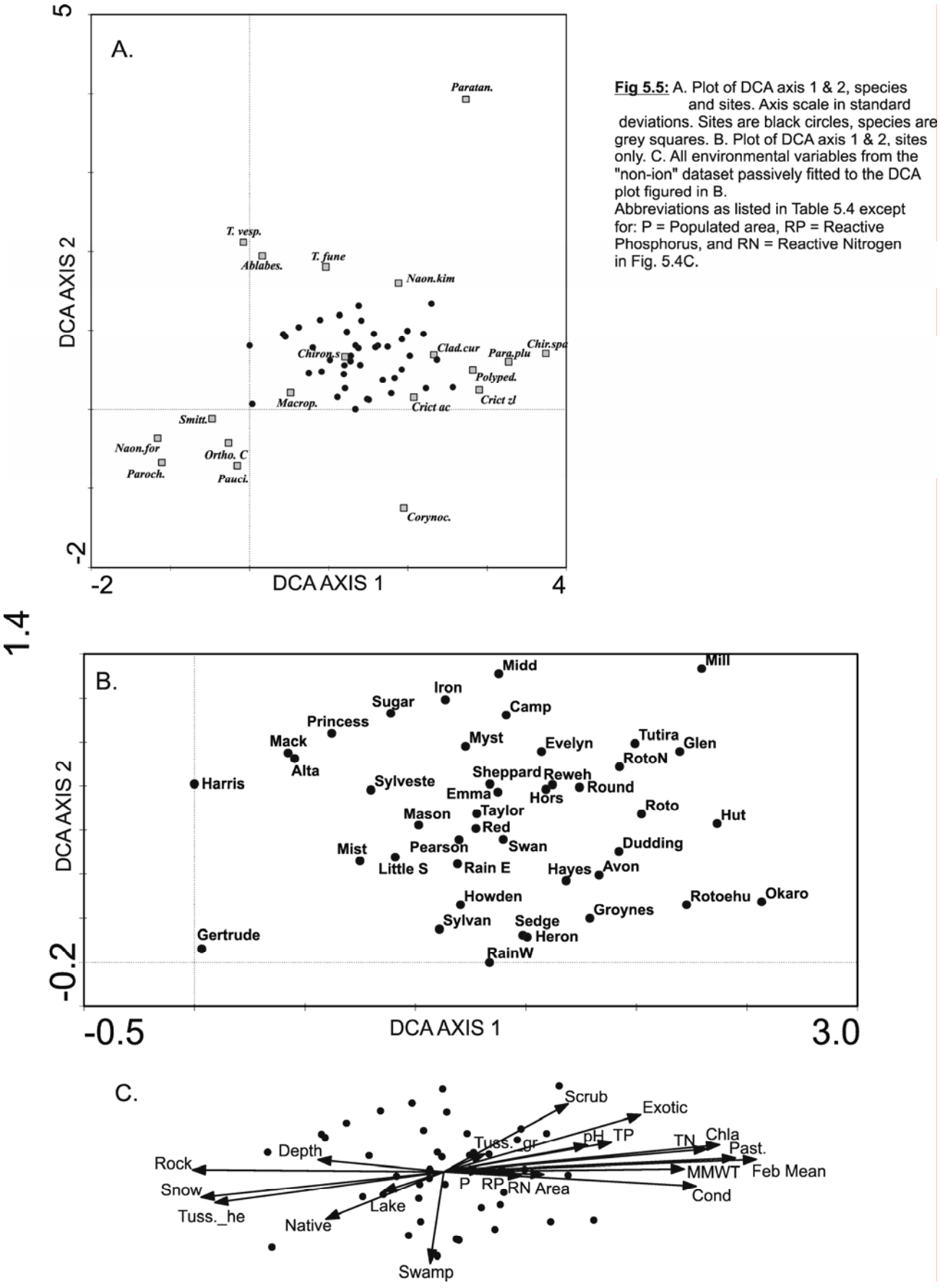


Fig 5.5: A. Plot of DCA axis 1 & 2, species and sites. Axis scale in standard deviations. Sites are black circles, species are grey squares. B. Plot of DCA axis 1 & 2, sites only. C. All environmental variables from the "non-ion" dataset passively fitted to the DCA plot figured in B.
Abbreviations as listed in Table 5.4 except for: P = Populated area, RP = Reactive Phosphorus, and RN = Reactive Nitrogen in Fig. 5.4C.

Constrained ordinations:

The gradient length of DCA axis 1 was 2.58 SD (**Table 5.5**). This lies above the suggested cut-off for linear ordination methods (2 SD) and below the suggested cut-off for unimodal methods (4 SD). Both methods were compared to test whether linear methods (RDA) or unimodal methods (CCA) were more appropriate. CCA captured slightly more of the variation in the chironomid taxonomic data compared to RDA. The cumulative percentage of the taxonomic data captured by the first two axes for CCA and RDA was 29.9 and 28.3% respectively. The first CCA axis captured 20% of the total variance in the chironomid species data, while RDA only captured 17%. Therefore CCA was selected as the most appropriate method in this case. Both CCA axes were significant ($P < 0.01$).

Partial CCAs were used to determine which environmental variable(s) explained the highest most statistically significant amount of variance in the chironomid species data. In the case of the "non-ion" dataset all 24 environmental variables were assessed using a series of partial CCAs. The majority of the environmental variables had extremely high variance inflation factors (VIFs >30). It was suspected that this was because of the catchment variables were themselves dependent on temperature (e.g. native forest at lower altitudes, tussock herbfield at higher altitudes). The catchment variables should also be highly correlated to the limnological variables (TN, Chla, conductivity). This was discussed in **Section 5.1.1** and is also evident in the correlation matrix provided in **Tables C1** and **C2** in **Appendix C**. The partial CCAs confirmed this suspicion, and this is discussed in the following text.

Only 9 of the 24 environmental variables displayed a statistically significant ($P \leq 0.01$) relationship to chironomid species variance (**Table 5.6**). A series of partial CCAs were run to determine which environmental variables contributed to a minimal adequate model that explains the greatest significant amount of the total species variance. The explanatory power and significance of the individual environmental variables provided in **Table 5.6** is misleading. A variable may appear to explain a significant amount of variance in the taxonomic data when in reality it is correlated to another variable with a true relationship to the variance in the taxonomic data. The explanatory power of an individual variable by itself can be called the *marginal effect*. A more reliable indication of whether these variables contribute to explaining the taxonomic variance is provided by the *conditional effect* (ter Braak and Šmilauer, 2002). The conditional effect is determined by partialling out the effect of other significant environmental variables. For example, the percentage of pasture in the catchment (Past.) appears to explain 15.6% of the total variance in the taxonomic data (**Table 5.6**). A correlation matrix for the nine significant environmental variables was created using a RDA

Variable	Covariable	λ_1/λ_2	P	Cum %	Outliers
Febmean	None	0.847	0.001	14.9	
MMWT	None	0.565	0.001	10.6	5, 6
Cond	None	0.848	0.001	13.5	
pH	None	0.216	0.15	4.3	14, 17, 29, 40
Depth	None	0.250	0.014	5	
Nox-N	None	0.106	0.656	2.1	1, 23, 18, 42
React P	None	0.200	0.196	3.4	19, 23, 27
TN	None	0.639	0.001	10.8	39
TP	None	0.365	0.002	13.6	14, 19, 23
Chla	None	0.840	0.001	13.4	
Lat	None	0.124	0.321	3.1	1, 2, 4, 5, 6, 38
Long	None	0.532	0.001	9.7	
Native	None	0.143	0.33	2.8	17, 37
Tuss._he	None	0.203	0.049	4.5	7, 8, 9, 11
Tuss._gr.	None	0.187	0.06	4.2	
Rock	None	0.532	0.001	10.3	
Snow	None	0.515	0.001	10.4	
Scrub	None	0.174	0.115	3.7	
Past.	None	0.987	0.001	15.6	
Exotic	None	0.313	0.013	5.8	2, 3, 5, 6, 31, 33
Lake	None	0.076	0.803	1.6	12, 16
Swamp	None	0.094	0.531	2.1	12, 16, 46
Crops	None	0.344	0.022	6.9	19
Popul.	None	0.106	0.37	2.3	

Table 5.6: Results of partial CCAs of the 24 environmental variables available for the "non-ion" dataset for the entire 43 lake training set. The explanatory power (λ_1/λ_2: eigen value for axis 1/eigen value for axis 2), significance (P), cumulative percentage of taxonomic variance explained by axis 1 (Cum %) and the identity of lakes identified as outliers are listed. Variables that did **not** explain a significant amount of the species variance are highlighted with grey.

Feb Mean	1								
MMWT	0.844	1							
Cond	0.706	0.709	1						
TN	0.660	0.470	0.611	1					
TP	0.258	0.350	0.389	0.512	1				
Chla	0.726	0.722	0.664	0.623	0.360	1			
Long	0.515	0.527	0.293	0.289	0.141	0.687	1		
Rock	-0.897	-0.652	-0.576	-0.610	-0.188	-0.550	-0.298	1	
Past.	0.698	0.723	0.644	0.505	0.354	0.717	0.616	-0.430	1
	Feb Mean	MMWT	Cond	TN	TP	Chla	Long	Rock	Past.

Table 5.7: Correlation matrix for a RDA of entire training set including the 9 environmental variables with significant marginal effects.

in CANOCO 4.5 (**Table 5.7**). It is clear that Past. is highly correlated with temperature (both Feb Mean and MMWT), Cond, and Chla. When the effect of Cond and Chla are partialled out (**Table 5.8),** Past. explains a small (3.4%) insignificant (P = 0.22) amount of the variance in the chironomid taxonomic data.

Only Feb Mean and TP remained significant after the remaining environmental variables were partialled out in a series of CCAs (**Table 5.8**). The effects of the other trophic variables (TN and Chla) and conductivity are confounded. The significance and explanatory power of MMWT, Long, Rock, and Past. were dramatically reduced after partialling of the trophic variables, conductivity and Feb Mean. Past. also had a detrimental effect on the performance of the trophic variables, and conductivity, but I believe this is because it is highly correlated to all of them (**Table 5.7**). The resulting CCA biplot in **Fig. 5.6** is constrained only to Feb Mean, Cond, TP, and Chla. The

Variable	Covariable	λ_1/λ_2	P	cum %
Feb Mean	None	0.847	0.001	14.9
	MMWT	0.494	0.001	9.1
	Cond	0.601	0.001	9.3
	TN	0.505	0.001	8.1
	TP	1.000	0.001	13.5
	Chla	0.481	0.001	8.1
	Long	0.465	0.001	9
	Rock	0.522	0.001	9.1
	Past.	0.550	0.001	8.5
MMWT	None	0.663	0.001	11
	Febmean	0.251	0.016	4.9
	Cond	0.171	0.26	3
Cond	None	0.891	0.001	14.4
	Feb Mean	0.492	0.002	7.7
	MMWT	0.357	0.004	6.3
	Both temp	0.386	0.003	6.6
	TN	0.282	0.015	5.1
	TP	0.475	0.002	8.3
	Chla	0.315	0.007	5.9
	Long	0.670	0.001	10.7
	Rock	0.733	0.001	10.8
	Past.	0.188	0.173	3.5
	Trophic	0.227	0.185	3.7

Variable	Covariable	λ_1/λ_2	P	cum %
TN	None	0.822	0.001	13.1
	Feb Mean	0.371	0.001	6.1
	MMWT	0.397	0.002	7.1
	Both temp	0.519	0.001	8.5
	Cond	0.256	0.03	4.6
	TP	0.437	0.002	7
	Chla	0.239	0.045	4.4
	Other trophic	0.165	0.474	2.6
	Long	0.592	0.001	9.8
	Rock	.133/.187	0.001	10.2
	Past.	0.201	0.129	3.8
TP	None	0.876	0.001	14.5
	Feb Mean	0.887	0.001	12.9
	MMWT	0.704	0.001	11.4
	Both temp	0.890	0.001	12.4
	Cond	0.490	0.001	8.5
	TN	0.484	0.001	7.8
	Chla	0.606	0.001	10.1
	Long	0.978	0.001	14.3
	Rock	1.127	0.001	14.5
	Past.	0.472	0.002	8.2
Chla	None	0.813	0.001	13.4
	Feb Mean	0.383	0.001	6.9
	MMWT	0.379	0.001	7
	Both temp	0.371	0.001	6.8
	Cond	0.260	0.017	4.9
	TP	0.530	0.001	9
	TN	0.252	0.021	4.7
	Past.	0.155	0.277	3

Variable	Covariable	λ_1/λ_2	P	cum %
Long	None	0.296	0.007	5.9
	Feb Mean	0.161	0.148	3.5
Rock	None	0.532	0.001	10.3
	Feb Mean	0.229	0.049	4.5
	MMWT	0.302	0.005	5.9
	Both temp	0.170	0.193	3.4
Past.	None	0.987	0.001	15.6
	Feb Mean	0.606	0.001	9.8
	MMWT	0.491	0.001	8.7
	Both temp	0.535	0.001	9
	Cond	0.311	0.008	5.9
	TN	0.373	0.001	7
	TP	0.588	0.001	10
	Chla	0.327	0.004	6.1
	Chla & Cond	0.184	0.220	3.4
	Trophic	0.010	0.088	4.1

Table 5.8: Results of a series of partial CCAs for each of the significant environmental variables for the entire training set. Both temp = Feb Mean and MMWT; Trophic = all trophic variables (TP, TN, Chla). Variables that did **not** explain a significant amount of the species variance are highlighted with grey.

other four variables have been added as supplementary variables to the CCA biplots. TN was not included as a constraining environmental variable as the canonical coefficients were insignificant for CCA axis 1, 2, and 3. The four constraining environmental variables explain 28.7% of the total variance in the taxonomic data. This figure was calculated from the sum of the canonical eigen values from a CCA constrained to the four environmental variables (0.383) divided by the total inertia (1.336) (**Table 5.9**). The total inertia in a unimodal method is the total variance in the taxonomic data as measured by the chi-square statistic of the sample-species table divided by the table's total (ter Braak and Šmilauer, 2002). Feb Mean explained the greatest amount of the total variance (7.0%) followed by Chla (4.9%), TP (3.8%), and Cond (2.9%). The interaction of all the variables accounted for 10% of the total variance (**Fig. 5.7**).

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.211	0.092	0.05	0.031	1.336
Species-environment correlations :	0.895	0.738	0.657	0.611	
Cumulative percentage variance					
of species data :	15.8	22.7	26.4	28.7	
of species-environment relation:	55.1	79	92	100	
Sum of all eigenvalues					1.336
Sum of all canonical eigenvalues					**0.383**

Table 5.9: The results of a CCA constrained to 4 environmental variables. St Anne's Lagoon and "Hut" have been removed from the final analysis as they were identified as outliers.

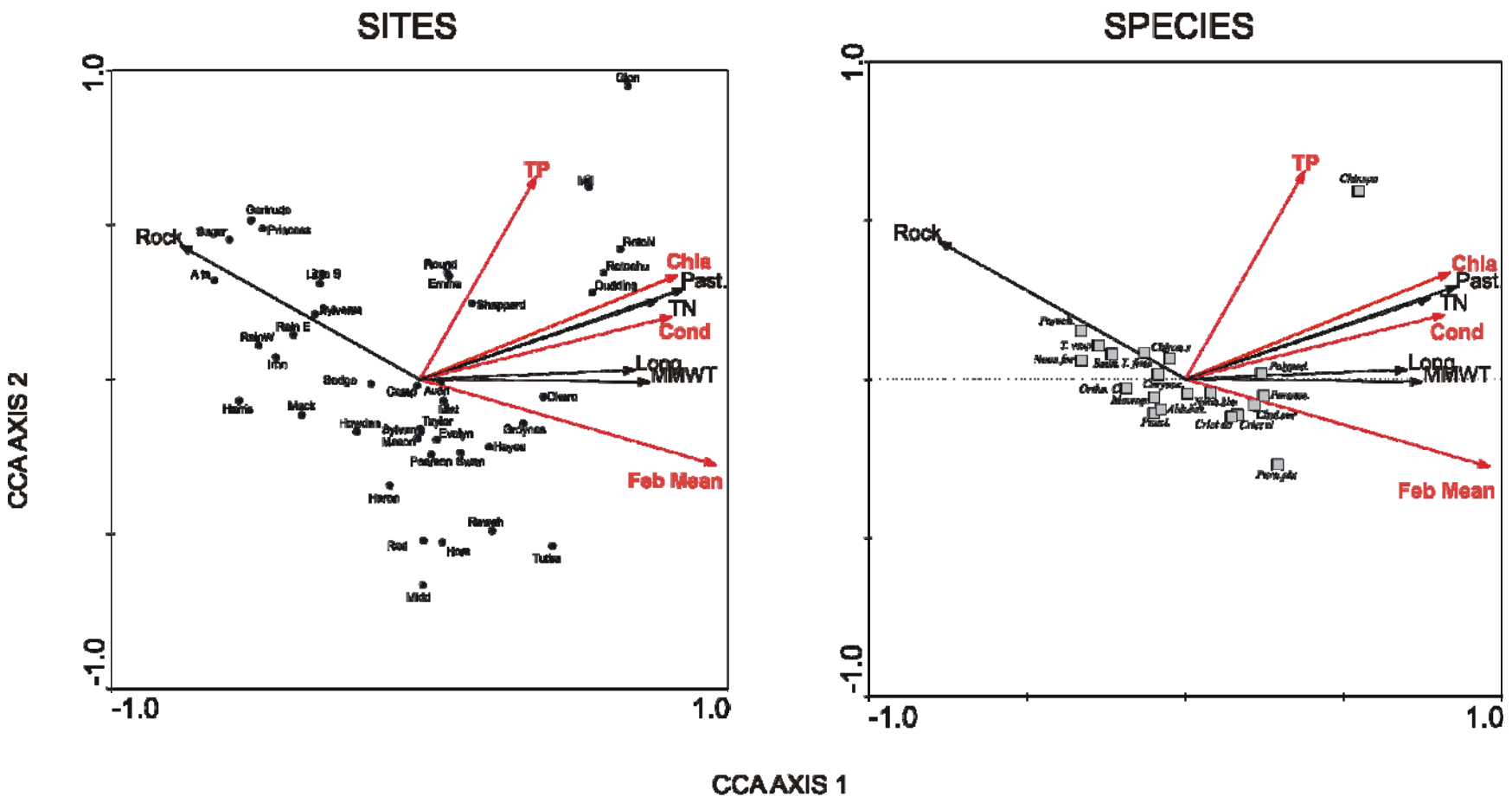


Fig. 5.6: CCA bi-plots of sites and species, constrained to 4 environmental variables (red arrows). Other variables have been fitted passively to the data as supplementary environmental variables (black arrows). St Annes Lagoon, Lake Rotorua S, and "Huf" were identified as an outliers (due to high values of TP and Cond) and were removed from the final CCA plot. Abbreviations for sites, species and environmental variables provided in Table 5.4. Only Feb mean and TP have a conditional effect that is significant to P<0.01.

	Intra-set correlations			Canonical coefficients			Approximate t-values		
Feb Mean	0.7953	-0.4735	0.1974	0.5845	-1.28	-0.2732	**4.0135**	**-4.9444**	-0.8091
Cond	0.7507	0.0314	0.3464	0.1222	0.2291	-0.8424	0.9199	0.9706	**-2.7362**
TP	0.5582	0.2942	-0.3646	0.0781	0.4225	-0.6265	0.7911	**2.4061**	**-2.7353**
Chla	0.8134	0.0825	0.0574	0.2245	0.7938	1.1149	1.7398	**3.4605**	**3.7263**
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3

Table 5.10: Intra-set correlations, canonical coefficients, and approximate t-values from a CCA of the entire dataset constrained to 4 environmental variables. Significant correlations between an environmental variable and each CCA axis (absolute t-value > 2.1) are in bold text.

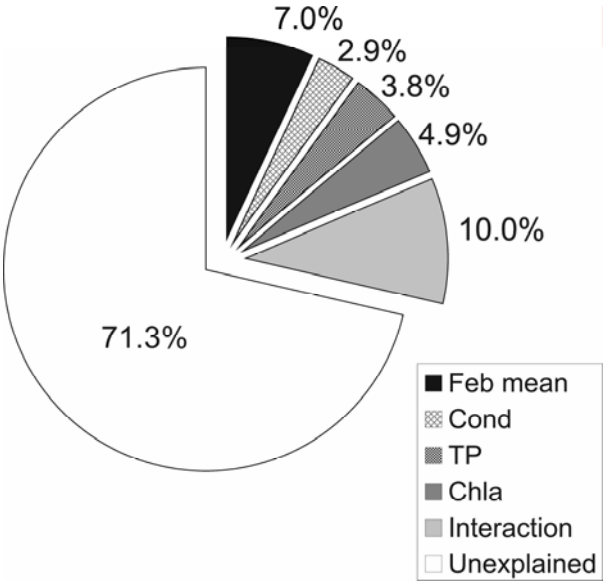


Fig. 5.7: Variance partitioning for the 4 environmental Variables retained for a minimum adequate Model for explaining the total species variance from the entire training set.

Based on approximate t-values of the canonical coefficients (**Table 5.10**) Feb Mean was significantly correlated with CCA axis 1 and 2, while TP and Chla were significantly correlated to CCA axis 2 and 3. Cond was significantly correlated to CCA axis 3. CCA axis 1 therefore represents a temperature gradient, while CCA axis 2 represents the combined effect of Feb Mean, Chla, and TP. CCA axis 3 is a trophic (Chla and TP) and conductivity gradient.

Parochlus spp., *Naonella forsythi* and *Tanytarsus vespertinus* are typical of cold, unproductive (low Chla) lakes. *Polypedilum* spp., *Paratrichocladius* sp., *Paratanytarsus* sp. and *Cladopelma curtivalva* are typical of warmer more productive (high Chla) lakes. Macropelopini, *Paucispinigera* sp., and *Ablabesmyia* sp. are typical of non-disturbed, un-productive lakes, while *Chironomus* sp a is typical of eutrophic to hypertrophic more saline (high Cond) lakes.

B. Removal of disturbed sites:

Because of the high degree of colinearity in the entire training set, 12 lakes were removed from the 43 lake training set because of high percentages of pasture ("Past."), exotic trees ("Exotic"), and crops ("Crops"). All of these lakes also had extremely high values for Cond and Chla. All of the lakes removed from the temperature training set are circled and marked with a "D" in **Fig. 5.1**. *Paratrichocladius pluriserialis* was also removed from this training set as it was no longer present above the cut-off abundance (2%) after the removal of the disturbed lakes.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.331	0.178	0.102	0.068	1.638
Lengths of gradient :	2.396	1.956	1.864	1.441	
Cumulative percentage variance of species data :	20.2	31.1	37.3	41.5	
Sum of all eigenvalues					1.638

Table 5.11: DCA results for temperature training set (n =31).

The remaining dataset comprised 31 lakes. A DCA of the taxonomic data for this reduced dataset produced a gradient length of 2.4 SD for axis 1 (**Table 5.11**). Once again this suggests the use of either linear (RDA) or unimodal methods (e.g. CCA) (ter Braak, 1995). CCA was selected as the preferred method as it explained a slightly higher amount of the total chironomid species variance. 10 environmental variables displayed a significant relationship to chironomid taxonomic

Variable	Covariable	λ_1/λ_2	P	cum %	Outliers
Feb Mean	none	0.911	0.001	14.9	
MMWT	none	0.383	0.004	8.1	
Cond	none	0.310	0.026	6.6	25
pH	none	0.189	0.175	4.4	29, 40
Depth	none	0.418	0.005	8	
NOX-N	none	0.159	0.292	3.7	18
React P	none	0.310	0.009	6.9	27
TN	none	0.435	0.001	8.5	35, 39
TP	none	0.174	0.21	4.1	29
Chla	none	0.412	0.002	8.5	18
Lat	none	0.183	0.206	4.1	3
Long	none	0.376	0.007	7.7	3
Native	none	0.150	0.317	3.6	17, 37
Tuss._he	none	0.439	0.002	8.7	7, 8, 9, 11
Tuss._gr	none	0.363	0.011	7.2	
Rock	none	0.774	0.001	12.9	
Snow	none	0.797	0.001	12.7	
Scrub	none	0.227	0.09	5.2	
Past.	none	0.261	0.03	5.5	
Exotic	none	0.307	0.025	6.4	
Lake	none	0.070	0.9	1.7	12, 16
Swamp	none	0.133	0.514	3	12, 27, 46
Crops	none	N/A	N/A	N/A	N/A
Popul.	none	N/A	N/A	N/A	N/A

Table 5.12: Results of partial CCAs for the chironomid taxonomic data from the 31 lake temperature training set constrained to the 24 "non-ion" dataset environmental variables separately. Variables that did **not** explain a significant amount of the species variance are highlighted with grey.

variance in the reduced temperature training set (**Table 5.12**). Of these 11 environmental variables only Feb Mean remained significant ($P \leq 0.01$) after all other variables except for "Rock" (% of rock in the catchment) were partialled out (**Table 5.14**). A RDA with the 10 significant environmental variables entered as both species and environmental data was performed to produce a correlation matrix (**Table 5.13**). "Rock" shows a high degree of negative correlation with Feb Mean (-92.9). Partialling out "Rock" from Feb Mean is equivalent to partialling out the effect of itself, hence the reduction in performance. When Feb Mean is partialled out from the effect of "Rock", the significance and explanatory power of this variable is drastically reduced (**Table 5.14**).

Feb Mean	1										
MMWT	0.737	1									
Cond	0.454	0.481	1								
Depth	-0.243	0.050	-0.190	1							
React P	-0.211	0.001	-0.017	-0.274	1						
TN	0.619	0.213	0.366	-0.557	-0.020	1					
Chla	0.501	0.366	0.239	0.002	-0.399	0.355	1				
Long	0.218	-0.053	-0.140	-0.025	-0.529	0.084	0.520	1			
Tuss._he	-0.773	-0.464	-0.381	0.293	0.128	-0.696	-0.481	-0.098	1		
Rock	-0.929	-0.682	-0.446	0.142	0.134	-0.609	-0.495	-0.138	0.807	1	
Snow	-0.552	-0.159	-0.114	0.319	0.501	-0.384	-0.483	-0.506	0.421	0.529	1
	Feb Mean	MMWT	Cond	Depth	React P	TN	Chla	Long	Tuss._he	Rock	Snow

Table 5.13: Correlation coefficients from an RDA of the 11 significant variables for the temperature training set

Variable	Covariable	λ_1/λ_2	P	cum %
Feb Mean	none	0.911	0.001	14.9
	MMWT	0.713	0.001	12.1
	Cond	0.682	0.001	11.9
	Depth	0.842	0.001	13.3
	React P	0.852	0.001	14.8
	TN	0.548	0.001	9.8
	Chla	0.720	0.001	12.9
	Long	0.837	0.001	14
	Tuss._he	0.500	0.001	8.8
	Tuss_gr	0.586	0.001	10.4
	Rock	0.192	0.223	4.1
	Snow	0.589	0.001	9.8
	Scrub	0.872	0.002	14.3
MMWT	none	0.383	0.004	8.1
	Feb Mean	0.273	0.092	5
Cond	none	0.310	0.026	6.6
	Feb Mean	0.166	0.469	3.2
Depth	none	0.418	0.005	8
	Feb Mean	0.360	0.024	6.2
	Both temp	0.328	0.053	5.8
React P	none	0.310	0.009	6.9
	Chla	0.202	0.224	4.4
	Feb Mean	0.355	0.013	6.7
	Both temp	0.340	0.03	6.6

Variable	Covariable	λ_1/λ_2	P	cum %
TN	none	0.435	0.001	8.5
	Feb Mean	0.153	0.557	3
Chla	none	0.412	0.002	8.5
	Feb Mean	0.325	0.031	6.3
	Both temp	0.347	0.027	6.8
	React P	0.216	0.225	4.7
Long	none	0.376	0.007	7.7
	Feb Mean	0.367	0.018	6.6
	Both temp	0.301	0.077	5.7
	React P	0.227	0.132	4.9
Tuss._he	none	0.439	0.002	8.7
	Feb Mean	0.110	0.849	2.1
Rock	none	0.774	0.001	12.9
	Feb Mean	0.090	0.93	1.8
Snow	none	0.797	0.001	12.7
	Feb Mean	0.426	0.008	7.4
	Both temp	0.291	0.094	5.2

Table 5.14: Results of a series of partial CCAs for the 11 environmental variables that displayed an apparent significant relationship to chironomid species variance. Variables that did **not** explain a significant amount of the species variance are highlighted with grey.

	Intra-set correlations			Canonical coefficients			Approximate t-values		
Feb Mean	-0.8656	0.0188	-0.463	-0.594	-0.2017	-1.1185	**-4.3766**	-1.1233	**-4.2983**
Depth	0.6102	0.3733	-0.4269	0.326	0.1062	-0.4022	**2.5921**	0.638	-1.6679
React P	0.3318	-0.8458	-0.0655	0.0943	-0.8171	0.2075	0.6641	**-4.3485**	0.7623
Chla	-0.4658	0.6307	0.0589	0.0687	0.5507	0.2792	0.5114	**3.096**	1.0835
Snow	0.8145	-0.21	-0.3787	0.3531	0.3538	-0.8122	**2.1303**	1.6133	**-2.5562**
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3

Table 5.15: Intra-set correlations, canonical coefficients, and approximate t-values for the 5 constraining variables from The temperature training set. Feb Mean is the variable most highly correlated to CCA axis 1, while React P Is most highly correlated to CCA axis 2. Both Feb Mean and "Snow" are significantly correlated to CCA axis 3. Significant t-values (> 2.1) are highlighted in bold.

"Depth" (maximum lake depth), React P, Chla, and "Snow" (% of snow and ice in the catchment) were also included as constraining variables in the final CCA plot. These variables were significant to $P < 0.05$ after Feb Mean was partialled out (**Table 5.14**) and all variables were significantly correlated with CCA axis 1 or 2 (**Table 5.15**). Feb Mean, depth, react P, Chla, and "Snow" together explained 34.5% of the total variance in the chironomid taxonomic data in the temperature training set (**Table 5.16**, **Fig. 5.9**). Feb Mean explained the largest amount (8%) of the total taxonomic variance, followed by React P (4.2%) and "Snow" (4%). The interaction between the 5 environmental variables accounted for 11.4% of the total taxonomic variance (**Fig. 5.9**). A large proportion of this (6.3%) could be accounted for by the interaction between Feb Mean, "Snow", and "Depth". This was determined by partialling out the effect of React P and Chla when Feb Mean, "Snow", and "Depth" were entered as environmental variables in a partial CCA in CANOCO 4.5. CCA axis 1 is predominantly a temperature (Feb Mean) gradient (**Table 5.15**). "Depth" and "Snow" are also correlated to CCA axis 1. In this context these variables also reflect the effect of temperature (water temperature) and this will be discussed in Section 5.2. CCA axis 2 is a productivity gradient.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.179	0.07	0.054	0.023	0.996
Species-environment correlations :	0.893	0.832	0.719	0.615	
Cumulative percentage variance					
of species data :	18	25	30.4	32.8	
of species-environment relation:	52.2	72.6	88.4	95.2	
Sum of all eigenvalues					0.996
Sum of all canonical eigenvalues					**0.343**

Table 5.16: results for a CCA with sites and species constrained to the 5 significant variables depicted in the CCA biplots in Fig. 5.8.

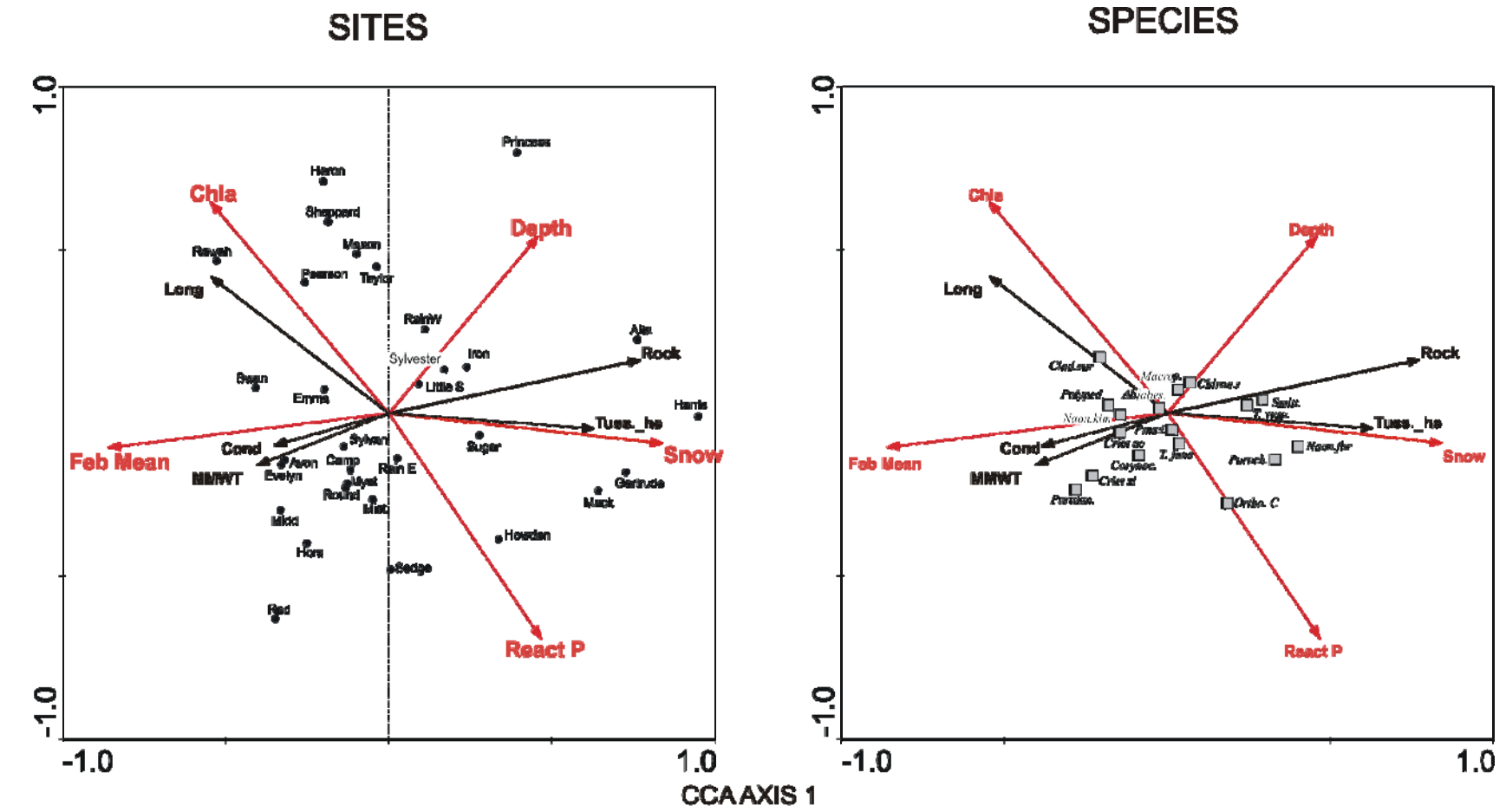


Fig. 5.8: CCA bi-plots of sites and species for the chironomid species data constained to 5 environmental variables (red arrows). Other variables have been fitted passively to the data. February mean (Feb Mean) is the only constraining variable that is significant to P = 0.001.

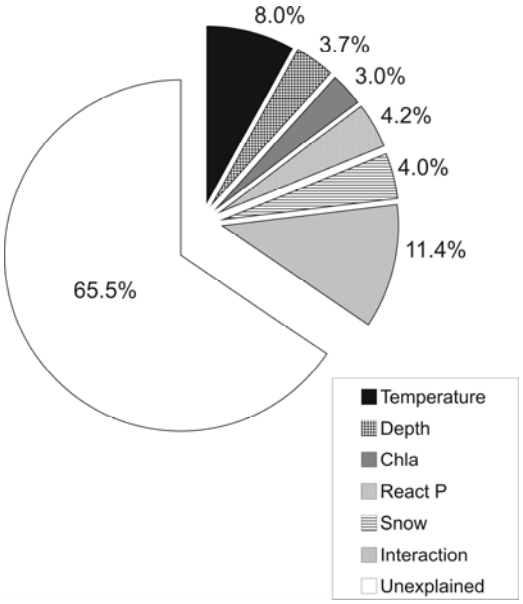


Fig. 5.9: Variance partitioning for the 5 environmental Variables retained for a minimum adequate Model for explaining the total species variance from the temperature training set.

Chla is positively correlated to CCA axis 2, while React P is negatively correlated to CCA axis 2. In the CCA biplot (**Fig. 5.8**) *Naonella forsythi*, Orthoclad species C, *Parochlus* sp., *Smittia* sp., and *Tanytarsus vespertinus* appear to be typical of the high altitude cold lakes. *Cricotopus aucklandensis*, *Naonella kimihia*, *Polypedilum* spp., and *Cladopelma curtivalva* are typical of low altitude warmer lakes. *Corynocera* sp., Orthoclad species C appears to be typical of un-productive lakes, while *Cladopelma curtivalva* is typical of more productive lakes (**Fig. 5.8**).

C. Removal of high altitude sites:

11 lakes were removed from the 43 lake training set because they had February mean temperatures below the arbitrary cut-off of 12ºC (**Fig. 4.5**, **5.1**). This dataset (the productivity/chemistry training set) has the lakes situated in disturbed catchments included.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.301	0.115	0.08	0.043	1.052
Lengths of gradient :	1.977	2.15	1.255	0.946	
Cumulative percentage variance of species data :	28.6	39.5	47.1	51.2	
Sum of all eigenvalues					1.052

Table 5.17: DCA results for the chironomid taxonomic data from the productivity/chemistry training set.

An initial DCA revealed that the gradient length for DCA axis 1 was low (1.977 SD) (**Table 5.17**) which suggests that linear methods should be appropriate in this case. However, a CCA and an RDA were performed to compare the results. The RDA explained less (53.3%) of the total variance of the chironomid taxonomic data than the CCA, which explained a total of 54.4%. The first RDA axis explained less of the chironomid species variance (18.2%) than the first CCA axis, which explained 22.2% (**Tables 5.18** and **5.19**). A Monte Carlo test revealed that the first RDA axis was not significant (P = 0.201). Both CCA axes were significant (P =0.001). Therefore unimodal methods were used to test the explanatory power and significance of the environmental variables in this case.

Axes	1	2	3	4	Total variance
Eigenvalues :	0.182	0.129	0.09	0.052	1
Species-environment correlations :	0.941	0.865	0.791	0.758	
Cumulative percentage variance of species data :	18.2	31.1	40.1	45.3	
of species-environment relation:	34.1	58.3	75.2	84.9	
Sum of all eigenvalues					1
Sum of all canonical eigenvalues					**0.533**

Table 5.18: Results of a RDA of the productivity/chemistry training set constrained to 13 environmental variables

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.221	0.09	0.087	0.06	0.996
Species-environment correlations :	0.954	0.901	0.718	0.825	
Cumulative percentage variance of species data :	22.2	31.3	40	46	
of species-environment relation:	40.7	57.3	73.2	84.3	
Sum of all eigenvalues					0.996
Sum of all canonical eigenvalues					0.544
Total variance explained					**0.546**

Table 5.19: Results of a CCA of the productivity/chemistry training set constrained to 13 environmental variables

Variable	Covariable	λ_1/λ_2	P	cum %	Outliers
Febmean	None	0.618	0.001	12.9	None
MMWT	None	0.496	0.001	10.3	1, 5, 6
Cond	None	0.857	0.001	16.3	25
pH	None	0.292	0.032	6.8	None
Depth	None	0.181	0.174	4.5	5, 16, 27, 42
Nox-N	None	0.260	0.148	5.7	23, 30, 42
React P	None	0.297	0.102	5.6	19, 23, 27
TN	None	1.011	0.001	16.1	None
TP	None	0.959	0.001	10.5	14, 19, 23
Chla	None	0.750	0.001	13.4	None
Lat	None	0.266	0.033	6.7	None
Long	None	0.381	0.004	9	None
Native	None	0.222	0.112	5	None
Tuss._her	None	0.178	0.182	4.6	None
Tuss._ gr	None	0.408	0.003	8.9	None
Rock	None	0.094	0.695	2.4	None
Snow	None	0.106	0.524	2.8	None
Scrub	None	0.100	0.605	2.7	None
Past.	None	0.980	0.001	14.6	None
Exotic	None	0.171	0.189	4.5	None
Lake	None	0.123	0.447	3.2	None
Swamp	None	0.143	0.306	3.7	None
Crops	None	N/A	N/A	N/A	St Annes
Popul.	None	0.106	0.416	2.9	None

Table 5.20: Results of partial CCAs for the productivity/chemistry training set.
Variables that did **not** explain a significant amount of the species variance are highlighted with grey.

8 environmental variables had a significant (P <0.01) relationship to the chironomid species variance after a series of partial CCAs. Past. and Cond had the largest marginal effect on the species variance, explaining 17.7 and 19.1% of the taxonomic variance (**Table 5.22**). An initial CCA including all 8 significant environmental variables identified St Anne's Lagoon, Mystery Tarn, and Lake Rotorua S as outliers due to extreme values of TP, Cond, TN respectively. Swan Lagoon was also removed because it was identified as a multivariate outlier, with more than three times the average leverage.

The results from a series of partial CCAs (**Table 5.21**) reveal that Feb Mean, MMWT, Past., and Tuss._gr were no longer significant (P <0.01) after all other significant environmental variables were partialled out. The results from the remaining four environmental variables seem to indicate that the effect of the trophic variables (TN, TP, and Chla) conductivity are confounded. Conductivity appears to remain significant when all three trophic variables are partialled out individually (**Table 5.21**). However, the conductivity gradient is highly correlated to temperature, TN, TP, and Chla (**Table 5.22**). Partialling out the effect of the trophic variables had a much more detrimental effect on the explanatory power and significance of conductivity than partialling out the effect of conductivity did to the trophic variables (**Table 5.21**). Further support for this argument is provided in the discussion in **Section 5.2.3**.

Variable	Co-variable	λ_1/λ_2	P	Cum%
Feb mean	None	0.600	0.001	12.8
	Cond	0.191	0.446	3.6
	TN	0.259	0.197	4.9
	TP	0.514	0.009	9.4
	Chla	0.214	0.219	4.6
	Past.	0.124	0.711	2.6
MMWT	Feb Mean	0.084	0.880	2
	Cond	0.196	0.486	3.6
	TN	0.546	0.005	9.1
	TP	0.300	0.058	6.1
	Chla	0.162	0.548	4.2
	Past.	0.141	0.616	2.9
Cond	None	1.097	0.001	19.1
	Feb Mean	0.571	0.001	11.2
	MMWT	0.580	0.001	11.4
	Temp	0.527	0.002	10.8
	TN	0.486	0.001	10
	TP	0.453	0.006	9.4
	Chla	0.516	0.001	10.3
	TN,Chla	0.321	0.027	7
	All trophic	0.345	0.159	5.1
TN	None	0.944	0.001	16.3
	Feb Mean	0.616	0.001	13.5
	MMWT	0.646	0.001	13.1
	Cond	0.261	0.079	5.6
	TP	0.344	0.025	7.6
	Chla	0.442	0.002	8.8

Variable	Co-variable	λ_1/λ_2	P	Cum%
TP	None	0.633	0.001	11.9
	Feb mean	0.831	0.001	15
	MMWT	0.651	0.002	12.9
	Temp	0.565	0.001	11.5
	Cond	0.446	0.005	9
	TN	0.168	0.569	3.7
	Chla	0.517	0.002	10.3
	Past.	0.494	0.001	9.9
Chla	None	0.716	0.001	13.4
	Feb Mean	0.241	0.149	5
	MMWT	0.204	0.192	5
	Cond	0.179	0.337	3.8
	TN	0.379	0.008	8.7
	TP	0.442	0.002	9.8
	Past.	0.318	0.009	8.1
All trophic	None	3.306	0.001	15.5
	Cond	1.388	0.096	7
Tuss._gr	None	0.4435	0.001	9.7
	Feb Mean	0.222	0.153	4.9
	MMWT	0.095	0.776	2.3
	Cond	0.175	0.361	3.7
	TN	0.395	0.001	8
	TP	0.302	0.049	6.1
	Chla	0.187	0.296	3.9
Past.	None	1.029	0.001	17.7
	Feb Mean	0.181	0.103	5.4
	MMWT	0.218	0.059	6.1
	Temp	0.161	0.164	4.9
	TN	0.247	0.041	7.2
	TP	0.364	0.004	10.3
	Chla	0.346	0.012	8.8
	TN, TP, Chla	0.253	0.079	5.8

Table 5.21: partial CCAs of the 9 significant environmental variables from the productivity/chemistry training set. The variable "All trophic" refers to0 the combined effect of TN, TP, and Chla. Variables that did **not** explain a significant amount of the species variance are highlighted with grey.

Feb Mean	1							
MMWT	0.801	1						
Cond	0.564	0.608	1					
TN	0.448	0.250	0.513	1				
TP	0.335	0.369	0.514	0.737	1			
Chla	0.736	0.712	0.658	0.495	0.446	1		
Tuss._gr	-0.533	-0.622	-0.456	-0.095	-0.268	-0.474	1	
Past.	0.817	0.677	0.656	0.427	0.414	0.673	-0.695	1
	Feb Mean	MMWT	Cond	TN	TP	Chla	Tuss._gr	Past.

Table 5.22: Correlation co-efficients for the 9 significant environmental variables from the productivity/chemistry training set.

All four environmental variables (Cond, TN, TP, and Chla) explained 32.6% of the total variance in the chironomid taxonomic variance (**Table 5.23**, **Fig. 5.10**). TN accounted for most (5%) of the explained variation. Based on canonical coefficients and approximate t-values from a CCA constrained to these four environmental variables (**Table 5.24**), TN was the environmental variable

with the most significant correlation to CCA axis 1, while TP, and Chla were the variables most highly correlated to CCA axis 2. Therefore CCA axis 1 is primarily a nutrient (TN) gradient.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.243	0.045	0.032	0.02	1.044
Species-environment correlations :	0.94	0.744	0.561	0.574	
Cumulative percentage variance					
of species data :	23.3	27.6	30.6	32.6	
of species-environment relation:	71.5	84.6	94	100	
Sum of all eigenvalues					1.044
Sum of all canonical eigenvalues					**0.34**

Table 5.23: The results of a CCA of the productivity/chemistry training set constrained to 4 significant environmental variables

	Intra-set correlations			Canonical coefficients			Approximate t-values		
Cond	0.7961	0.0082	0.478	0.4414	-0.2852	1.2014	**4.2629**	-1.1861	**2.9374**
TN	0.8589	-0.2619	-0.3271	0.7	0.1826	0.0638	**5.1389**	0.5775	0.1186
TP	0.6583	-0.5916	-0.4176	-0.1483	-0.9964	-0.6425	-1.1377	**-3.2925**	-1.248
Chla	0.7568	0.4802	-0.2293	0.1916	0.9594	-0.7773	1.789	**3.8579**	-1.8374
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3

Table 5.24: Intra-set correlations for a CCA of the two environmental variables that were retained in the final minimal adequate model for the productivity/chemistry training set. TN is the variable with the strongest, most siginifcant correlation to CCA axis 1. All significant t-values (> 2.1) are highlighted in bold.

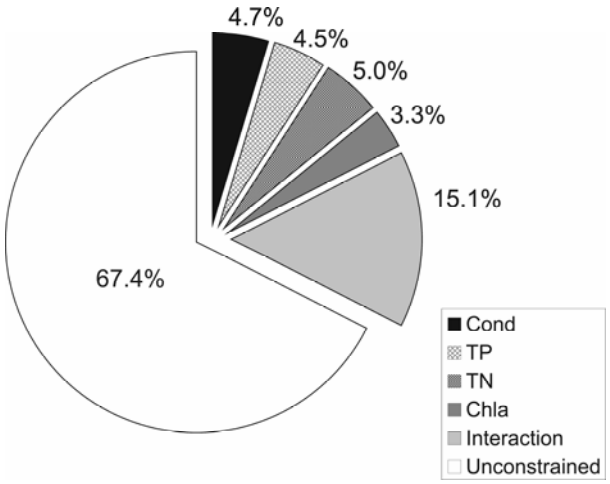


Fig. 5.10: Proportion of the total chironomid taxonomic Variance explained by conductivity, TP, TN, And Chla in the productivity/ chemistry training set.

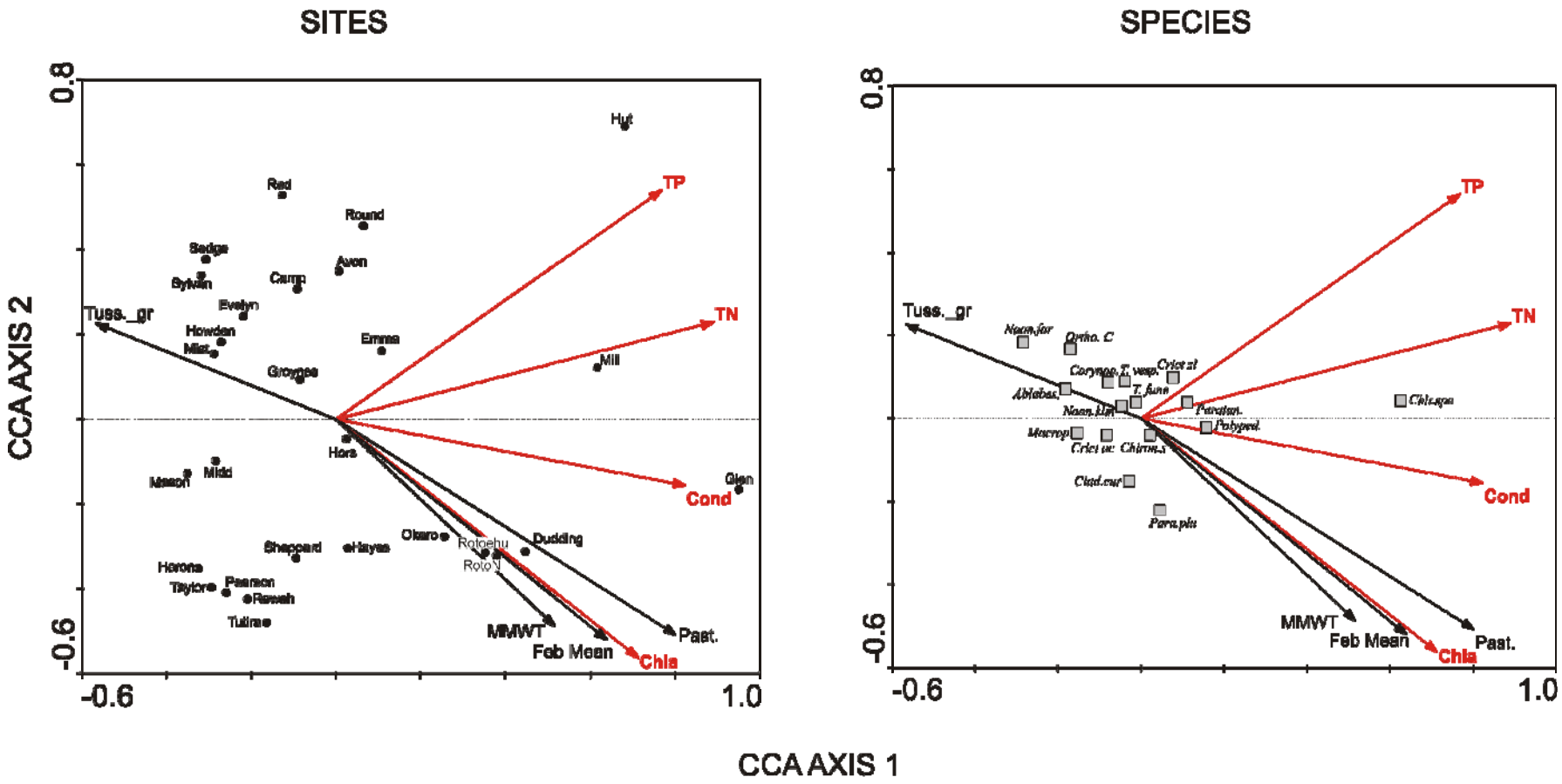


Fig. 5.11: CCA bi-plots of sites and species for the chironomid species data constrained to the 4 significant environmental variables for the productivity/chemistry training set (red arrows). Other environmental parameters (black arrows) have been fitted passively to the CCA plot. St Anne's Lagoon, Mystery Tarn, and Roto have been removed because they were identified as outliers in the final CCA due to extreme values of TP, Cond, TN respectively. Swan was also removed as it was identified in CANOCO 4.5 as a multivariate outlier, with more than three times the average leverage.

The Macropelopini, *Naonella forsythi* and *Ablabesmyia mala* were located furthest to the left of CCA axis 1 in the CCA biplot depicted in **Fig. 5.11**, and are therefore typical of lakes with a low trophic status (oligotrophic, trophic definition after Burns et al., 2000). *Chironomus* sp. a was located furthest to the right on CCA axis 1 and is therefore the taxon that is typical of eutrophic to supertrophic water bodies.

5.2 DISCUSSION

5.2.1 The relationship between catchment type and limnology

It is obvious from the PCA biplot in **Fig. 5.1** and the correlation matrix in **Appendix C** that there is a trend of increasing trophic level (TP, TN, Chla concentrations) and conductivity (salinity) with decreasing altitude. The trend towards increasing lake productivity at lower altitudes is likely to be a combination of the natural tendency towards high nutrient concentrations at lower altitudes (Riera et al., 2000) and the increased human impact (agriculture etc.) in the lowland catchments in this training set. Landscape position (altitude and slope) exerts an influence on runoff, drainage and soil development (Aandahl, 1948), thus affecting the influx of dissolved ions and nutrients. The quantities of phosphorus entering surface drainage vary with the amount of phosphorus in soils, topography, vegetative cover, and quantity and duration of runoff flow (Wertzel, 2001).

Chlorophyll *a* (Chla) concentration provides a proxy for phytoplankton production, which is influenced by temperature and nutrient availability (phosphorus and nitrogen) (Wetzel, 2001). There was still a high degree of correlation between Chla and temperature (Feb Mean) even after the removal of disturbed sites (**Table 5.13**). Other studies that have sought to exclude disturbed sites from biological training sets (e.g. Larocque et al., 2001) have noted a high degree of correlation between lake elevation and lake productivity. It is logical that the warmer temperatures at lower altitudes would encourage higher phytoplankton productivity.

The tendency towards an increase in conductivity at lower altitudes is also due to the effect of landscape position and climate. A high ratio of evaporation to precipitation will result in the concentration of dissolved solids in a water body. Many of the lakes located to the east of the Southern Alps (lakes 14, 19, 20, 21, 22, and 23, **Fig. 4.2**) were more saline, with values for electrical conductivity ranging from 173 to 381 µS/cm. All of these lowland lakes were also shallow (< 4m maximum depth) and situated in an area of low rainfall (Sturman and Wanner, 2001). Lake levels in

many of the lakes were particularly low in the lakes in this region in the 2003/2004 sampling period due to extremely low rainfall during that summer sampling season. The drought-induced low lake levels were exacerbated in two of these lakes (20 & 22) as these are also subject to draw-down for farm irrigation.

The ionic concentrations for most of these lakes (**Fig. 5.12**) are consistent with those recorded from typical marine/coastal precipitation (Wertzel, 2001), with Na^+, Cl^-, and SO_4^{--} being the dominant ions.

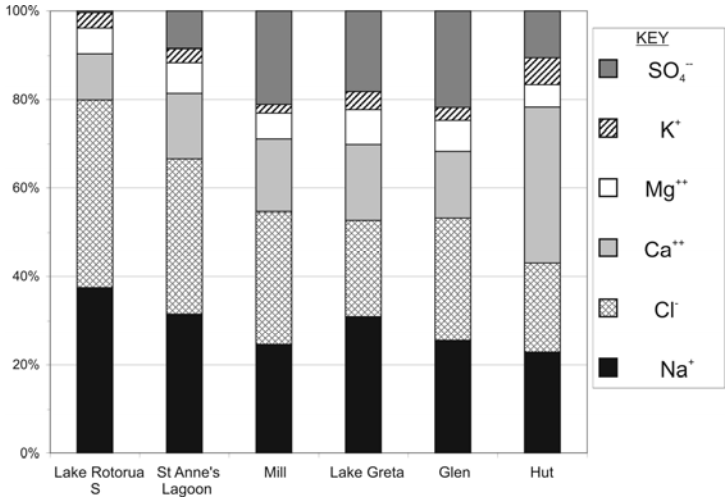


Fig. 5.12: Ionic concentrations of the more saline lakes on the eastern coastal plains of the South Island. Y axis represents relative proportion of each ion in terms of mg/L.

Lake Rotorua S had the highest proportions of the ions Na^+ and Cl^- (**Fig. 5.12**) which is not surprising as this lake is the closest to the coast (ca. 2.5 km to the west). Ca^{++} ions are also common in marine/coastal precipitation (Wertzel, 2001), but the high proportion of Ca^{++} ions, particularly in "Hut" (Lake 23, **Table 4.1**) could also be sourced from windblown dust from the west, where there are large exposures of calcareous sedimentary rocks (Gregg, 1964).

The high correlation between chlorophyll *a* (Chla) and conductivity (Cond) (**Table C1** and **C2**, **Appendix C**) is partially due to the fact that many of the more saline lakes were also situated in farmed catchments. The percentage of pasture in the catchment was the catchment characteristic with the highest positive correlation with TN (0.4) and TP (0.34). Both TN and TP were highly correlated to Chla, with correlation coefficents of 0.64 and 0.4 respectively. White et al. (1985) also found that TN explained a greater proportion of the variation in the Chla concentrations than TP in 12 volcanic plateau lakes in the North Island of New Zealand. White (1983) suggested that the relatively low concentrations of nitrogen in New Zealand waters may lead to biomass limitation by that nutrient in some situations.

High concentrations of Na^+ are also likely to encourage the growth of cyanobacteria as it is a requirement for the process of photosynthesis, bicarbonate transport, pH regulation and nitrogen fixation in this phylum (Allem and Arnon, 1955). A threshold of 4 mg/L Na^+ is required for near optimal growth of some species of cyanobacteria (Wetzel, 2001). A series of partial RDAs were performed to test which of the measured ionic concentrations explained the largest significant amount of variance in the concentration of Chla. The results of a series of partial RDAs are depicted in **Table 5.25**. Na^+ was the only ion to explain a reasonable proportion (>2%) of the variance in the Chla concentration after the effects of the other ions were partialled out individually. The explanatory power of Na^+ was most dramatically affected by partialling out the effect of Mg^{++}.

Variable	Co-variable	P	Cum%
SO_4^{--}	None	0.002	26.1
	Na^+	0.5	1.8
K^+	None	0.001	49.8
	Na^+	0.747	0.5
Cl^+	None	0.002	39.8
	Na^+	0.750	0.5
Mg^{++}	None	0.001	54.7
	Na^+	0.910	0
Na^+	None	0.001	62.2
	Cl^+	0.001	37.5
	K^+	0.004	24.9
	Mg^{++}	0.025	16.6
	SO_4^{--}	0.002	49.3

Table 5.25: The results of a series of partial RDAs to test the explanatory power of each of the ions on the variance in the concentration of chlorophyll *a*. Cum% = the cumulative percentage of the variance explained by the first RDA axis. The concentration of Na^+ explains the greatest amount of variation in the concentration of chlorophyll a when the effects of all other ions were partialled out individually.

Jeppesen et al. (1994) argue that the suppression of grazing zooplankton by high salinities could contribute to the establishment of large phytoplankton populations even in the presence of macrophytes. Large numbers of ephippia (resting stages) of the Cladoceran *Daphnia* were common in surface sediments in the highly productive brackish lakes in this training set. Cladocera are known to produce these resting stages to survive phases of unstable conditions and environmental stress, e.g., lake desiccation or lake freezing (Deng, 1996).

5.2.2 Chironomid taxonomic data

Chironomid taxonomic diversity was typically low (mean = 0.64), with only three sites with a diversity (H') greater than 1 (**Table B3 Appendix B**). Many studies from the Northern Hemisphere cite larger numbers of taxa and more diverse assemblages. Heiri and Lotter (2001) cite diversities (H') ranging from 0.44 to 1.309 in the 5 samples from the Swiss Alps they used in a study to test the

effect of low counts on reconstruction results. Larocque et al. (2001) recorded a total of 85 chironomid taxa from a 100-lake training set from northern Sweden. Of the 85 taxa, 48 had abundances ≥2% in at least two lakes. Walker and Mathewes (1989) report taxonomic diversities exceeding 2 in the lowland lakes in a set of lakes sampled in the southern Canadian Cordillera (**Fig. 5.13**). The taxonomic richness and diversity of the New Zealand assemblages is comparable with data recorded from a 54 lake Danish training set (Brodersen and Lindegaard, 1999). Brodersen and Lindegaard (1999) recorded 41 taxa. *Chironomus* (type *plumosus*) was also the most abundant taxon in the Danish training set.

The diversity of New Zealand benthic invertebrate communities (including the Chironomidae) is generally regarded as depauperate relative to the Northern Hemisphere (Ashe et al., 1987). Raven and Axelrod (1972) cite the small size of this country and the possible shortage of refuges during the Pleistocene glaciations as a possible cause for this. As I mentioned in **Chapter 2** the limited taxonomic diversity of the New Zealand chironomid larvae is likely to be caused to some degree by the state of the taxonomy of this group. The assemblages in this training set and the lakes sampled by Shakau (1996) and Boubée (1983) were dominated to a large extent by the Chironominae and the Macropelopini. At this stage there is an imbalance between the number of taxa described in the adult form and as larvae especially from these two groups (see **Chapter 2**). Revision of the taxonomy of the larvae will result in an increase in the diversity of chironomid assemblages in New Zealand.

There was a tendency towards low taxonomic richness and diversity (H') in the lowland and high altitude lakes, with a peak in the mid-altitude sites. This relationship between taxonomic richness and diversity and altitude (**Fig. 5.3A** and **B**) is due to different limiting factors at each altitudinal extreme (high vs low). Taxonomic richness and diversity is low in the lowland sites due to the number of lakes in the training set that were situated in disturbed catchments. The percentage of pasture in the catchment was most highly correlated to the concentration of chlorophyll *a* (**Table 5.7**). Many of the lowland lakes were also more saline, with conductivities exceeding 100 μS/cm. Salinity and productivity (via the concentration of dissolved oxygen) have been demonstrated to affect chironomid abundance and distribution (e.g. Walker et al., 1995; Lotter et al., 1998). The possible effects of these variables on the New Zealand chironomid fauna will be discussed in more detail later in this chapter. The indirect effect of these environmental parameters in limiting the growth of macrophytes is also likely to affect chironomid diversity. Previous studies by Stark (1981) have revealed the larger diversity of New Zealand macrophyte-associated fauna compared to the profundal fauna. The limited growth of macrophytes as well as low temperatures, and limited food

resources are also likely to limit the diversity of the high altitude chironomid fauna. The effect of temperature on the New Zealand Chironomidae will also be discussed later in this chapter.

The trend towards decreasing diversity in the lowland lakes observed in this study is likely to be the result of the predominance of intensive agriculture in the catchments of these lakes. If lowland lakes in undisturbed catchments had been sampled, it is likely that diversity would increase with respect to decreasing altitude (**Fig. 5.13**). This trend was observed by Walker and Mathewes (1989) in the southern Canadian Cordillera (**Fig. 5.13**). In the data set examined by Walker and Mathewes (1989) diversity (H') increased from less than 0.5 in alpine lakes (above 2000m) to a maximum of ca. 2.4 in the lowland lakes.

Many of the lakes sampled during this study were located in tussock grassland. Although not intensively farmed, this vegetation in many cases, results from anthropogenic deforestation; by the Polynesians between 1200 and 1400 AD and by the Europeans in the 19th century (Burrows and Russell, 1990; McGlone & Wilmshurst, 1999). Despite this fact, there was high variation in the diversity of the chironomid assemblages in lakes situated in tussock grassland. Red Lagoon, located in tussock grassland had one of the most diverse chironomid assemblages in the entire training set (**Fig. 5.3A**).

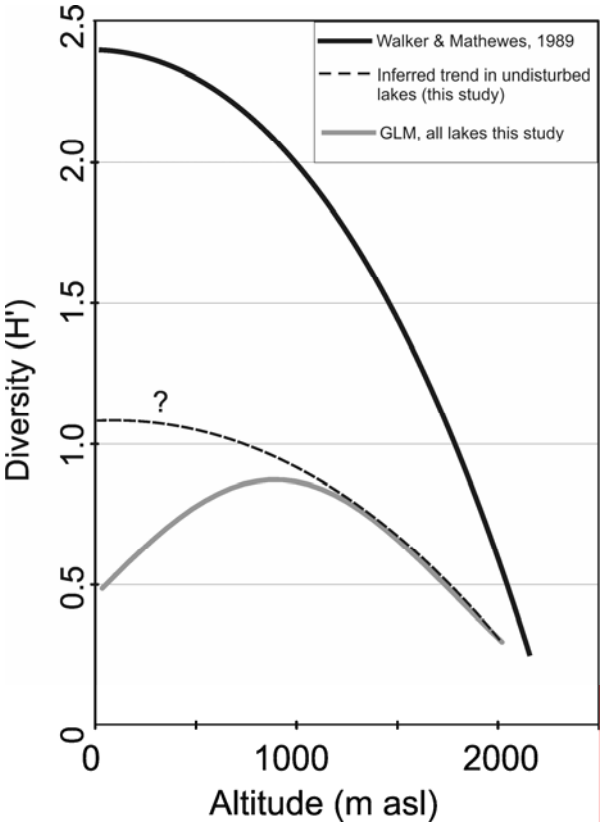


Fig. 5.13: GLM curve fitted to the taxonomic diversity of the chironomid assemblages from the entire training set (see **Fig. 5.3A**). This is compared to the trend in taxonomic diversity observed by Walker & Mathewes (1989). Walker & Mathewes (1989) observed an increasing diversity with respect to decreasing altitude. In this study there was a peak in diversity about 1000m amsl with a decreased diversity in the lowland sites. This is proably due to the eutrophic conditionof the lowland lakes in this study. The dashed line represents a possible scenario if undisturbed lowland lakes were sampled.

5.2.3 Exploratory analysis of the "non- ion" dataset

A. Entire dataset

Comparison of constrained and unconstrained ordinations:

The CCA of the entire training set, constrained to 5 environmental variables (**Fig. 5.6**) appears to adequately explain most of the taxonomic variance in DCA axis 1. This implies that the measured environmental parameters are indeed the main drivers of chironomid taxonomic variance. The first DCA axis explained 22.3% of the total chironomid variance, while the first CCA axis explained 15.8%. The site and species scores for DCA and CCA axis 1 were compared to investigate the relative positioning of the sites and taxa along the maximised artificial "environmental gradient' created by DCA and the constrained environmental gradient from CCA.
The positions of the species and sites relative to CCA axis 1 were very similar to their relative position to DCA axis 1. A linear regression of CCA site and species scores produced an excellent fit, with a correlation coefficient of 0.92 and 0.89 respectively (**Fig. 5.14** and **5.15**). Temperature (Feb Mean) was also the environmental variable that was most highly correlated to DCA species axis 1 (correlation coefficient = 0.852).

Conversely there was no one limnological variable that appeared to be highly correlated with DCA axis 2 when the environmental variables were fitted passively to the DCA plot (**Fig. 5.5C**). The catchment variable "Swamp" was most highly correlated with DCA axis 2, but the correlation coefficient was relatively low (-0.331). In the high altitude sites DCA axis 2 separated lakes with a higher proportion of Orthocladiinae and Podonominae and Macropelopini with lakes that were dominated by Tanytarsini (*T. vespertinus* and *T. funebris*) (**Fig. 5.5B**). The possible causes of this variation will be discussed later in this chapter. Both "Gertrude Saddle" and Lake Harris were taxonomically rich with a large proportion of Podonominae (particularly *Parochlus* spp.), and Orthocladiinae. This contrasts with the species poor assemblages from lakes such as "Sugarbowl Tarn" Princess Bath and Lake Alta, which were dominated by Tanytarsini and *Chironomus*.

In the mid altitude lakes there is a distinct separation along DCA axis 2 of *Corynocera* sp. (located towards the bottom) and *Naonella kimihia* (located near the top). Many of the lakes located towards the bottom of DCA axis 2 were shallow and clear with abundant macrophytes or allocthonous organic debris (plant material) e.g. Lake Sedgemere and "Rainbow Ski-field West".

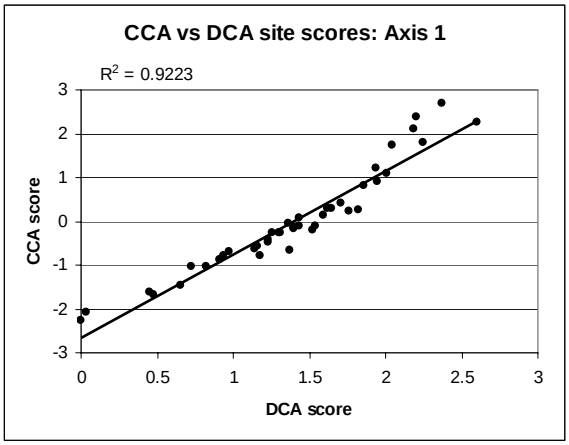


Fig. 5.14: Scatterplot of CCA site scores versus DCA site scores for axis 2 from the entire training set

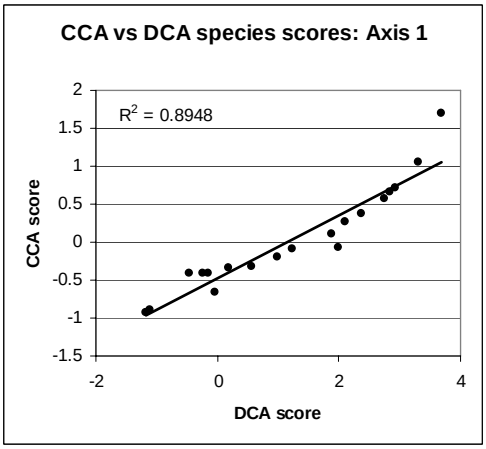


Fig. 5.15: Scatterplot of CCA species scores versus DCA species scores from axis 1 for the entire training set

There were a variety of different lake types situated towards the top of DCA axis 2. *Naonella kimihia* was most common in Lake Evelyn and Lake Middleton (ca. 60% relative abundance). Lake Evelyn was a shallow (3m) lake with abundant macrophytes and allochthonous organic debris (reeds, leaves) while Lake Middleton was slightly deeper (4.5m) and more turbid with abundant macrophytes. Boubée (1983) found *N. kimihia* exclusively associated with macrophytes during his collection of live larvae from some lakes from the central North Island. Schakau (1993) also considers *N. kimihia* "an indicator of macrophytes".

CCA axis 2 captured slightly less of the total taxonomic variation than DCA axis 2 (6.9% versus 9.8%) (**Table 5.5** and **5.9**). The correlation between the species and site scores for CCA axis 2 and the corresponding scores from DCA axis 2 was far weaker than for CCA axis 1 (**Fig. 5.16** and **5.17**), suggesting a shift in the relative positions of the species and sites with respect to the second ordination axis. Many of the sites (i.e assemblages) that were dispersed on DCA axis 2 were located in closer proximity on CCA axis 2. Despite the difference in positions of the sites and species along axis 2 in the CCA and DCA plots there is little difference between the total amount of taxonomic variation explained by the respective axes. However, the difference between the second ordination axes suggests that some other environmental variables that influence chironomid distribution (e.g. substrate, macrophyte type and abundance) have not been measured.

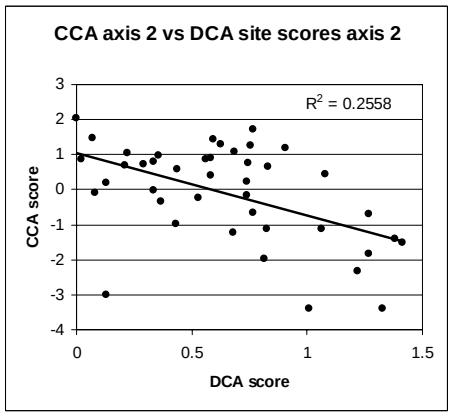


Fig. 5.16: Scatterplot of CCA site scores versus DCA site scores for axis 2 from the entire training set

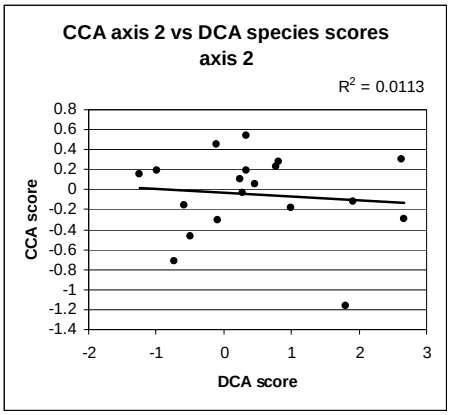


Fig. 5.17: Scatterplot of CCA species scores versus DCA species scores for axis 2 for the entire training set

Constrained ordinations:

Temperature (Feb mean) emerged as the variable that independently explained the highest (7%) proportion of the total taxonomic variation in the entire training set (**Fig. 5.7**). The main problem with the entire training set was the co-linearity of temperature, trophic level (TN, TP, and Chla), and conductivity (**Table 5.7**). As I mentioned in the previous section, this is partially due to the effect of lake position and more intensive farming in the lower altitude catchments. Although Feb Mean was the only variable with a significant relationship to CCA axis 1 (**Table 5.10**), Cond, Chla, TP, and TN still had a significant effect ($P < 0.01$) on the chironomid taxonomic variance after the effects of Feb Mean were partialled out (**Table 5.8**).

Despite the inclusion of productive (Chla > 5 µg/L) and more saline (conductivity > 100 µS/cm) lakes, temperature (Feb Mean) still contributes the highest (7%) independent contribution to the chironomid taxonomic variation of the measured environmental variables (**Fig. 5.7**). This is an important observation as it shows that the effect of large scale temperature fluctuations are likely to override the effect of changes in lake production and chemistry at this scale.

Brodersen and Quinlan (2006) argue that factors such as climate (temperature), food and oxygen availability have the greatest influence on chironomid larval growth and mortality. On smaller spatial and temporal scales food-web interactions (e.g. fish predation), micro-habitat conditions (e.g. substrate) are important limiting environmental parameters. Johnson and Goedkoop (2002) also argue that global, large scale patterns of climate ultimately control the structure of benthic

invertebrate communities in lakes. The data from this study suggests that the influence of climate (via temperature) has the most important large scale effect on the distribution of the New Zealand Chironomidae.

Chlorophyll *a* explained the second highest (4.9%) portion of the chironomid taxonomic variance (**Fig. 5.7**). The concentration of Chlorophyll *a* is likely to be a reflection of both food quantity and quality in shallow un-stratified lakes (Langdon et al., 2006) and dissolved oxygen concentration in deeper stratified lakes. Loss of oxygen from the hypolimnion results primarily from biological oxidation of organic matter, both in the water and at the sediment/water interface (Wetzel, 2001). Increased primary production (reflected by increased chlorophyll *a* concentration) will lead to more rapid hypolimnetic anoxia in deep stratified lakes.

Even though temperature was the dominant controlling environmental parameter influencing the chironomid taxonomic variance in this training set, the colinearity of the environmental gradients, exacerbated by the inclusion of disturbed, hypertrophic lowland lakes makes it impossible to determine the exact nature of the variation of chironomid assemblages to independent environmental parameters. All of the trophic variables (TN, TP, and Chla) plus conductivity were significant after the effect of temperature (Feb Mean) was partialled out (**Table 5.8**). Therefore I do not consider it possible to produce a reliable transfer function for temperature from the un-screened training set.

B. Removal of disturbed sites

February mean temperature (Feb Mean) emerged as the only variable in the "temperature training set" (n = 31) to retain a significant ($P < 0.01$) relationship to the chironomid taxonomic variance after all other environmental parameters were partialled out (**Table 5.14**). Feb Mean also contributed the largest proportion (8%) to the amount of explained variance in the taxonomic data in the temperature training set. This suggests that summer temperature is the most important limiting factor on the distribution of New Zealand Chironomidae. This is consistent with other temperature transfer functions developed from different regions around the world which have also selected mean summer temperature as the best temperature variable (e.g. Lotter et al., 1998; Lotter et al., 1999; Larocque et al., 2001). Chironomid assemblages are likely to be influenced by both air temperature (e.g., during pupation, flight, reproduction and dispersal (Hoffman 1986; Walker and Mathewes 1989b)) and water temperature (e.g., larval development rates and mortality (Robb 1966)). Walker et al. (1991) and Olander et al. (1997) have also demonstrated that there is a close relationship between air and water temperature for shallow polymictic lakes. I preferentially sampled shallow

lakes for the chironomid training set. The mean depth for the lakes sampled for the entire 46-lake training set was 13.6m (**Table 4.1**).

Even though several high altitude deep lakes were sampled (e.g. Lake Alta and Lake Harris) the effect of depth was reduced after the effect of air temperature was partialled out (P = 0.053). It does seem that even though the significance of the relationship between lake depth and chironomid taxonomic variance is low compared to air temperature, there is some effect in the high altitude (> 1600m) lakes. Lake depth and "Snow" (the percentage of snow and ice in the lake catchment) were included as constraining variables in the final CCA (**Fig. 5.8**). Deeper high altitude lakes such as Lake Harris, and lakes with a substantial amount of snow and ice in the catchment during summer (e.g. "Gertrude Saddle") had chironomid assemblages that included a significant proportion of taxa from the Orthocladiinae, Podonominae, and Diamesinae. Taxa belonging to these groups are typically common in rhithral (upland) streams and glacier fed brooks and are tolerant of cold (< 6 ºC) water temperatures (Pinder, 1995).

The shallower (< 15m) high altitude lakes (e.g. "Sugarbowl Tarn") typically contained higher proportions of Chironominae (*Chironomus* spp. and *Tanytarsus* spp.) and larvae belonging to the tribe Macropelopini. Walker and Mathewes (1989) observed a similar distinction between shallow high altitude 'ponds' (shallow waterbodies) and deep high altitude lakes altitudes in the southern Canadian Cordillera. The shallow high altitude ponds typically contained *Chironomus*, various Orthocladiinae, Tanypodinae, and Tanytarsini. The deep high altitude lakes were dominated by Orthocladiinae, Diamesinae, and Tanytarsini. The high altitude lakes and the high altitude ponds of Walker and Mathewes seem to have equivalent fauna to the orthoclad/*Parochlus* lakes (e.g. Lake Harris) and the Chironominae/Macropelopini lakes (e.g. "Sugarbowl Tarn") in New Zealand. Walker and Mathewes (1989) argue that the scouring of the littoral zone in large deep high altitude lakes, and the cold temperatures at depth, prevent the typical Chironominae/Tanypodinae assemblage of the shallow ponds from successfully colonizing these waterbodies.

It is therefore important to examine the performance of a temperature inference model derived from a training set containing large numbers of deep high altitude lakes, or lakes with a large contribution of melt-water over the summer. This also has implications for temperature reconstructions based on training sets where such lakes have been excluded. Brooks and Birks (2001) observed that two proglacial lakes in a 111-lake training set from north-west Europe contained large numbers of cold stenothermic taxa (e.g. *Diamesa*). The resulting transfer function for July air temperature under-predicted the temperature in these lakes by ca. 4 ºC. It is therefore important to cross-validate chironomid-based reconstructions with other proxies where there are

likely to be fluctuations in depth or a large input of melt-water into a lake. It is possible to estimate fluctuations in lake depth based on the fossil remains of macrophytes, but it may be more difficult to recognise the effect of the input of melt-water on chironomid-based temperature reconstructions.

February mean air temperature explained a total of 8% of the total chironomid taxonomic variance (**Fig. 5.9**). This apparently small contribution to the total taxonomic variance is comparable to the unique (conditional) effect of temperature reported by previous studies. Larocque et al. (2001) report that July temperature explained only 3.5% of the total taxonomic variance in a training set from northern Sweden after the effects of the water chemistry variables (e.g. pH, conductivity, etc) were partialled out. Larocque et al. (2001) produced a robust temperature transfer function from this training set, with an r^2_{jack} of 0.65 and an $RMSEP_{jack}$ of 1.13°C. Temperature reconstructions from four lakes in northern Sweden based on this transfer function compared favourably with meteorological records that extended back to 1910 AD. Therefore, even though there is a large amount of variation un-accounted for in the temperature training set, it is possible to create a robust temperature transfer function that produces reasonable temperature reconstructions.

Patterns of faunistic turnover with respect to temperature:

New Zealand sub-fossil chironomid assemblages showed marked changes in species composition corresponding to gradients of altitude and temperature (**Fig. 5.18**). Four main zones of faunistic turnover (based on 42 taxa) were produced in a zone analysis using the CONISS (Constrained Incremental Sum of Squares) function in Zone 1.2 (Juggins 1992). The main zone of faunistic change approximated the tree-line (~1000-1300 m). Other workers (e.g. Porinchu and Cwynar, 2000) have identified the tree-line as an important ecological boundary controlling chironomid distribution. Thus, although the abundance of many taxa is dramatically reduced above the tree-line (e.g. *Naonella kmihia*), many of these taxa continue to contribute to the chironomid assemblages up to the 10ºC air temperature limit (**Fig. 5.18**). This suggests that the actual thermal tolerance of many of the New Zealand chironomid taxa corresponds to a Feb Mean of ca. 10ºC but there are other environmental factors that are contributing to reduce their abundance above the tree-line. The lack of input of woody debris above the tree-line is likely to have a minor effect on the chironomid fauna above the tree-line. We only need to compare lakes situated in montane tussockland (e.g. Red Lagoon) with those situated in alpine tussock-land (e.g. Lake Harris). The chironomid assemblages are quite different from each of these lakes even though both lakes are situated in grassland. The abundance of *N. kimihia* begins to decline below the tree-line to ~ 10%, after which *N. kimihia* remains as part of the chironomid assemblages up to the 10ºC limit.

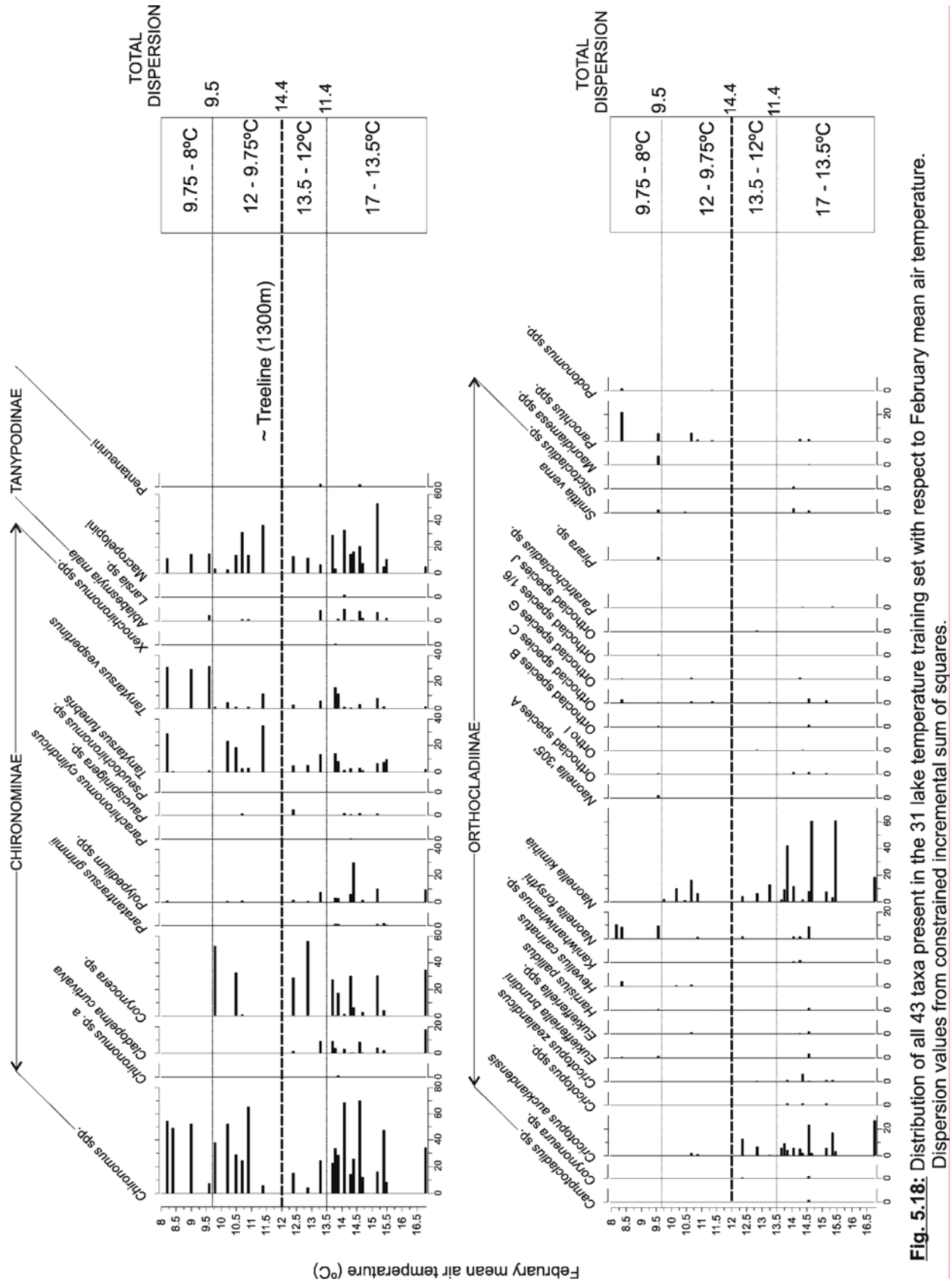


Fig. 5.18: Distribution of all 43 taxa present in the 31 lake temperature training set with respect to February mean air temperature. Dispersion values from constrained incremental sum of squares.

Heegaard et al. (2006) compared the rate of assemblage compositional change (using measures of dissimilarity) with respect to altitude for chironomids, Cladocera, and diatoms in the Swiss Alps. They found that the ecotonal region (zone of abrupt taxonomic turnover) was much wider for the chironomids, with an extension downwards from the tree-line with the relative abundances of several species beginning to decline below the tree-line. I observed the same pattern in my training set, with many taxa (including *N. kimihia*) declining in relative abundance below the tree-line. At this stage there is a paucity of lakes in this training set spanning the tree-line. Adding more lakes to the existing training set to increase the resolution across this important ecotone should be a priority for future work.

Many of the taxa that occur above the tree-line (particularly the Macropelopiini) are a major component of the chironomid assemblages of lowland oligotrophic lakes. Brodersen et al. (2004) found that cold-water assemblages in low-arctic West Greenland were dominated by oxy-conformers; chironomids incapable of surviving low concentrations of dissolved oxygen. All the main high altitude species (except *Chironomus*), were rare or absent in eutrophic lowland lakes (see **Fig. 5.20**); suggesting that this may also the case for the New Zealand fauna. The genus *Chironomus*, on the other hand, was also present in high concentrations in eutrophic lowland lakes. *Cladopelma curtivalva*, *Cricotopus zealandicus*, *Cricotopus aucklandensis*, and *Polypedilum* were characteristic of warm (>13^{o}C) temperatures. These genera (particularly *C. curtivalva* and *Polypedilum*) are also typical of warmer conditions in other parts of the world (Walker et al. 1991; Larocque et al. 2001).

C. Removal of high altitude sites

The results of the partial CCAs provided in **Table 5.21** and the canonical coefficients in **Table 5.24** seem to suggest that the effects of conductivity and trophic level on the chironomid taxonomic variance are confounded. Both conductivity and TN are highly correlated to CCA axis 1, and the explanatory power and significance of TN is drastically reduced by partialling out the effect of conductivity. I believe that in this training set the trophic gradient (lake production and nutrient concentration) is the true limiting factor in this case; I provide here three arguments for this interpretation in the following text.

1. Conductivity is highly correlated to all of the trophic variables with correlation coefficients exceeding 0.5 for chlorophyll a, TN, and TP (**Table 5.22**). Therefore it is to be expected that the significance of TN (itself a trophic variable) will be reduced when a variable that is highly correlated to itself and all the other trophic variables is partialled out.

2. One crucial piece of evidence is provided by examining the distribution of the chironomid taxa along the conductivity gradient in this training set. A diagram depicting the relative abundance of all 45 taxa in the productivity/chemistry training set with respect to the conductivity gradient is provided in **Fig. 5.19**. The faunistic turnover along this conductivity gradient was divided into four main zones based on a zone analysis using the CONISS (Constrained Incremental Sum of Squares) function in Zone 1.2 (Juggins, 1992). One of the most notable characteristics of the upper three zones is the gradual reduction in the abundance of *Chironomus* spp. and the increased abundance of *Chironomus* sp. a.. Robb (1966) observed a similar transition between these two larval types in a drainage ditch from one of the Bromley oxidation ponds in Christchurch New Zealand. The drainage ditch flowed from the oxidation pond into a brackish estuary. The salinity gradient along the drainage ditch ranged from 3.5 $^{0}/_{00}$ to 17.5 $^{0}/_{00}$. This interstitial salinity represented an average of the several measurements between high and low tide. Robb (1966) calculated the salinity based on the chlorinity of the water samples. The concentration of Cl^- was converted to salinity (the total salt concentration of the water expressed as parts per thousand $^{0}/_{00}$) by the equation that was in common use at the time:

$$\text{Salinity} = (\text{chlorinity} \times 1.805) + 0.03 \quad \text{(equation 1)}$$

In the settling pond the chironomid community comprised 96% *Chironomus* spp., "thummi' type (with ventral tubules). The relative abundance of the "thummi" type gradually decreased with increasing salinity until the community comprised 100% *Chironomus* "salinarius" type (lacking ventral tubules). Robb (1966) stated that there was a minimal variation in other environmental conditions (substrate, oxygen, etc.) along the ditch and therefore attributed the change to increased salinity. Laboratory experiments testing the salinity tolerance of the "thummi" and "salinarius" types confirmed that the *Chironomus* "salinarius" type had a higher tolerance for salinity. All first instar larvae of the "thummi" type died within 18 hours when exposed to salinities in excess of 7 $^{0}/_{00}$.

At the time the study was conducted by Robb (1966) it was believed that the "thummi" and "salinarius" types represented phenotypes of *Chironomus zealandicus*. Robb (1966) suggested that

exposure to high concentrations of salinity during a critical phase of egg embryology could be responsible for determining the phenotype. Subsequent work by Forsyth and Martin (unpublished, see **Chapter 2**) has revealed that the "thummi' and "salinarius" types do in fact represent distinct genotypes. For example *Chironomus novae-zealandiae* is of the 'thummi' type, while *Chironomus* sp. a is of the "salinarius" type. At the upper end of the conductivity gradient in this training set it is evident that the abundance of *Chironomus* sp. a is increasing, while the abundance of *Chironomus* spp. is decreasing, which is in keeping with the trend observed by Robb (1966). However, the problem is that the upper end of the salinity (conductivity) gradient observed in this training set is far too low to be responsible for the high abundances of *Chironomus* sp. a. The highest chlorinity (Cl^- concentration) in this training set was 0.049 g/L (**Table 5.26**). Using equation 1 (above) this converts to a salinity of 0.338 $^0/_{00}$, a value that is ca. $1/20^{th}$ of the upper threshold for the 'thummi' type determined by Robb (1966). Therefore I argue that lake trophy (production and nutrient concentrations) is the true limiting factor in the lakes that I have sampled.

LAKE NAME	Chlorinity	Chlorinity	Salinity	% seawater
Princess Bath	0.020	0.000	0.030	0.086
Rainbow Skifield E	0.190	0.000	0.030	0.087
Rainbow Skifield W	0.360	0.000	0.031	0.088
"Sugarbowl Tarn"	0.766	0.001	0.031	0.090
Lake Mistletoe	0.777	0.001	0.031	0.090
Lake Mackenzie	0.778	0.001	0.031	0.090
Lake Alta	0.811	0.001	0.031	0.090
Lake Harris	0.951	0.001	0.032	0.091
Lake Sedgemere	0.986	0.001	0.032	0.091
Lake Evelyn	1.058	0.001	0.032	0.092
Lake Middleton	1.082	0.001	0.032	0.092
Red Lagoon	1.209	0.001	0.032	0.092
Avon	1.230	0.001	0.032	0.092
Lake Camp	1.289	0.001	0.032	0.093
Lake Howden	1.336	0.001	0.032	0.093
Little Sylvester Lake	1.430	0.001	0.033	0.093
Lake Sylvester	1.460	0.001	0.033	0.094
Lake Sylvan	1.623	0.002	0.033	0.094
Mystery Tarn	1.637	0.002	0.033	0.095
Lake Emma	1.674	0.002	0.033	0.095
Iron Lake	1.780	0.002	0.033	0.095
Groynes	2.128	0.002	0.034	0.097
Lake Roundabout	2.900	0.003	0.035	0.101
Horseshoe Lake	3.098	0.003	0.036	0.102
Gertrude Saddle	4.093	0.004	0.037	0.107
Lake Johnson	4.336	0.004	0.038	0.109
Swan Lagoon	6.081	0.006	0.041	0.118
Lake Greta	14.542	0.015	0.056	0.161
Hut	16.923	0.017	0.061	0.174
Lake Rotorua S	23.702	0.024	0.073	0.209
Mill	29.748	0.030	0.084	0.240
Glen	45.233	0.045	0.112	0.320
St Annes Lagoon	48.618	0.049	0.118	0.338
	mg/L	g/L	$^0/_{00}$	

Table 5.26: Chlorininty values from the training set converted to salinity using the same calculation used by Robb (1966).

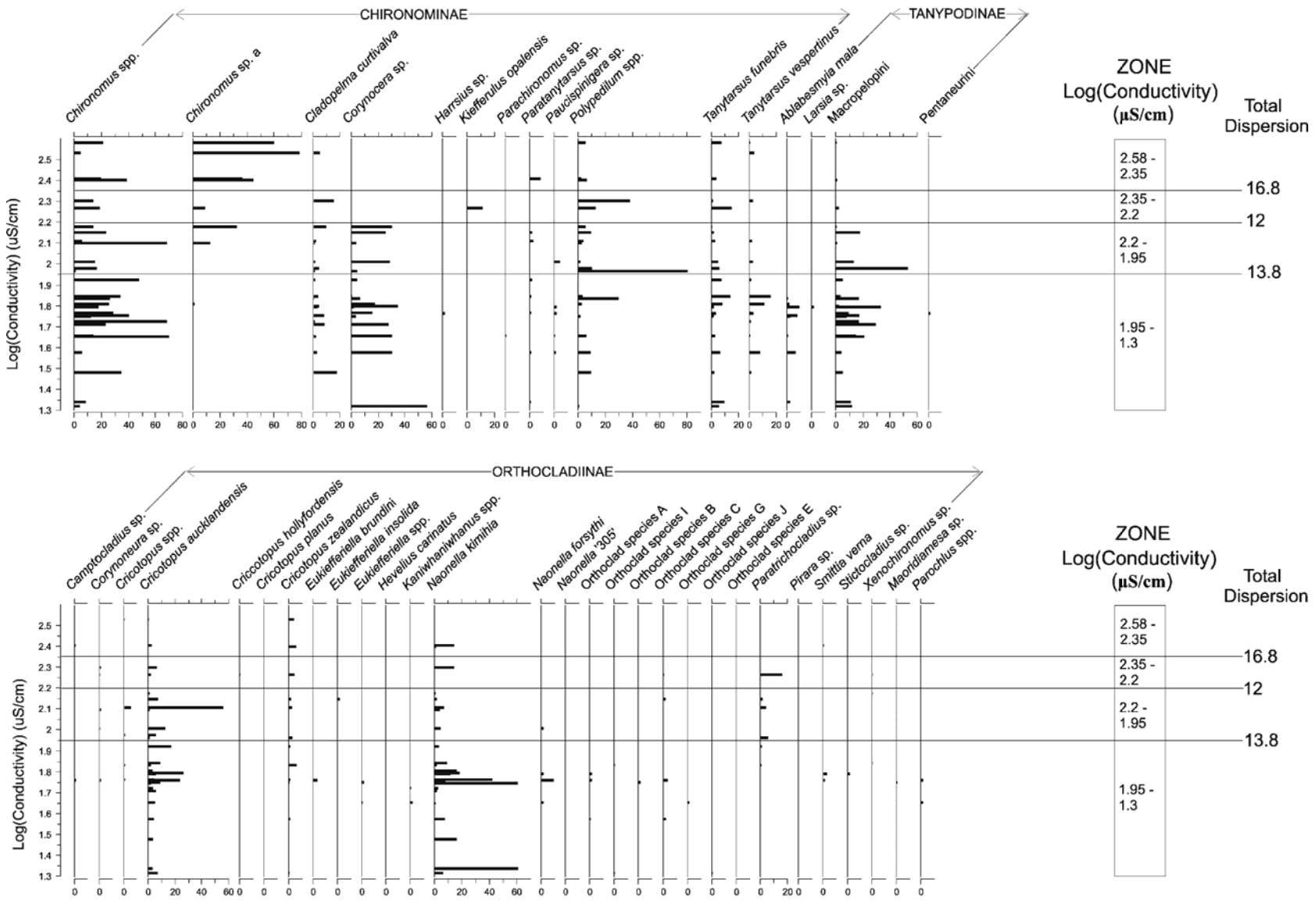


Fig. 5.19: Chironomid relative species abundances for the productivity/chemistry training set with respect to conductivity, including all 45 taxa. All outliers have been removed.

3. The salinity tolerance of the chironomid fauna from an 86 lake training set from western Canada (Walker et al., 1995) also lends support to this argument. Four chironomid salinity zones were recognised along the salinity gradient in this training set. The major switch from freshwater taxa assemblages to euryhaline assemblages occurred at a salininty of 10 g/L, which is equivalent to an electrical conductivity of ca. 10,000 µS/cm. The Tanytarsina, *Chironomus* sp., and Pentaneurini where relatively common up to this limit. Even some of the less tolerant genera (e.g. *Dicrotendipes*) were common up to a salinity of 1.3 g/L (ca. 1000 µS/cm). The abundance of taxa in this training set belonging to equivalent taxonomic groups (*Tanytarsus* spp., *Polypedilum* spp., *Chironomus* spp., and Macropelopini) begins to seriously decline at a threshold of ca. 160 µS/cm (**Fig. 5.19**). It is therefore unlikely that this is a true conductivity threshold.

Chironomid response to trophic status:

It is not surprising that the New Zealand chironomid larvae are sensitive to variations in lake trophic status. Previous studies have cited total phosphorus (TP), chlorophyll *a* (Chla) and total nitrogen (TN) (Brooks et al., 2001; Brodersen and Lindegaard, 1999 and Brodersen and Anderson, 2002 respectively) as important controlling variables for chironomid distribution. The trophic gradient represents changes in a number of environmental parameters that directly and indirectly effect chironomid larval survival. Biological productivity in the epilimnion (represented by Chla) is indicative of food availability and oxygen conditions (Lindegaard, 1995). Major reductions of dissolved oxygen in the lake hypolimnion are associated with bacterial decomposition of dissolved and sedimenting particulate organic matter (Seto *et al*., 1982). The concentration of TN represents ammonia (NH_4^+), hydroxylamine (NH_2OH), nitrite (NO_2^-), nitrate (NO_3^-), and dissolved and particulate organic nitrogen (Wetzel, 2001). The concentration of TN is therefore directly correlated to the consumption of oxygen, and indirectly as a nutrient limiting the biological production in many New Zealand lakes (White et al., 1983). The TN concentration was also found to more strongly correlated to the concentration of chlorophyll *a* in this training set (see **section 5.2.1**) suggesting that many of the lakes in this training set are also nitrogen limited.

Increasing lake trophic status is also likely to indirectly influence the composition of chironomid assemblages due to an effect on macrophyte growth. Submerged vegetation functions as a substrate, protection, a food source, and increases sediment stability (Pinder, 1986). Increased nutrient inputs to ultra-oligotrophic lakes may result in increased macrophyte growth, encouraging the proliferation of chironomids that are typically associated with macrophytes. Further increases in nutrient input,

and an associated increase in lake-water turbidity are likely to reduce macrophyte abundance reducing the abundance of the macrophyte associated fauna. This is likely to be an important factor effecting the New Zealand chironomid fauna in New Zealand as the largest contribution to the taxonomic richness in the lowland lakes is derived from macrophyte associated fauna (Stark, 1981).

Patterns of faunistic turnover with respect to total nitrogen:

The relative abundances of all 43 taxa enumerated from the productivity/chemistry training set with respect to the TN gradient is provided in **Fig. 5.20**. The trophic level definitions of Burns et al. (2000) are also provided to place the TN concentrations in context. The Burns et al. (2000) trophic level classification scheme is based on annual average TN concentrations. The TN values were derived from spot samples taken during the summer in this study, and are likely to over-estimate the trophic status of the lakes with respect to this classification system.

Chironomus sp. a is typical of highly productive lakes, as it is also tolerant of saline conditions (Robb, 1966). A similar pattern occurs in training sets from other parts of the world (e.g. Walker et al., 1995; Little and Smol, 2001). It seems that the physiology of this genus enables it to cope with a broad range of salinities and eutrophic conditions. Several physiological adaptations allow the *Chironomus* genus to survive prolonged periods of anoxia. The presence of haemoglobin in the haemolymph, and the ability to reduce metabolic rates and switch to anaerobic metabolism are important (Hamburger et al., 1994, 1995). The ability to maintain osmotic and ionic regulation as metabolites from anaerobic metabolism build up is also a key to surviving prolonged periods of anoxia (Scholz and Zerbst-Boroffka, 1998), and will also enable *Chironomus* to survive extreme and fluctuating salinities.

The Macropelopini, *Corynocera* sp., and *Cricotopus aucklandensis* were the most common chironomid fauna in the oligotrophic lakes. Surprisingly, Swan Lagoon had a high abundance (ca 50%) of head-capsules belonging to the tribe Macropelopini despite having one of the highest TN concentrations in the entire training set (**Fig. 5.20**). Lake levels were particularly low when the surface sediment sample was collected. Abundant deposits of macrophytes were also observed washed up on the shore of this lake. This evidence along with the chironomid assemblage suggests that the trophic status of the water at the time of sampling does not represent a typical state for this lake. It is also likely that variation in TN concentrations occurs throughout the summer in the rest of the training set, but this lake represents an extreme example. *Naonella kimihia* was particularly common in the mesotrophic lakes. This follows as it has been observed in previous studies that this taxon is typically associated with macrophytes (Boubee, 1983).

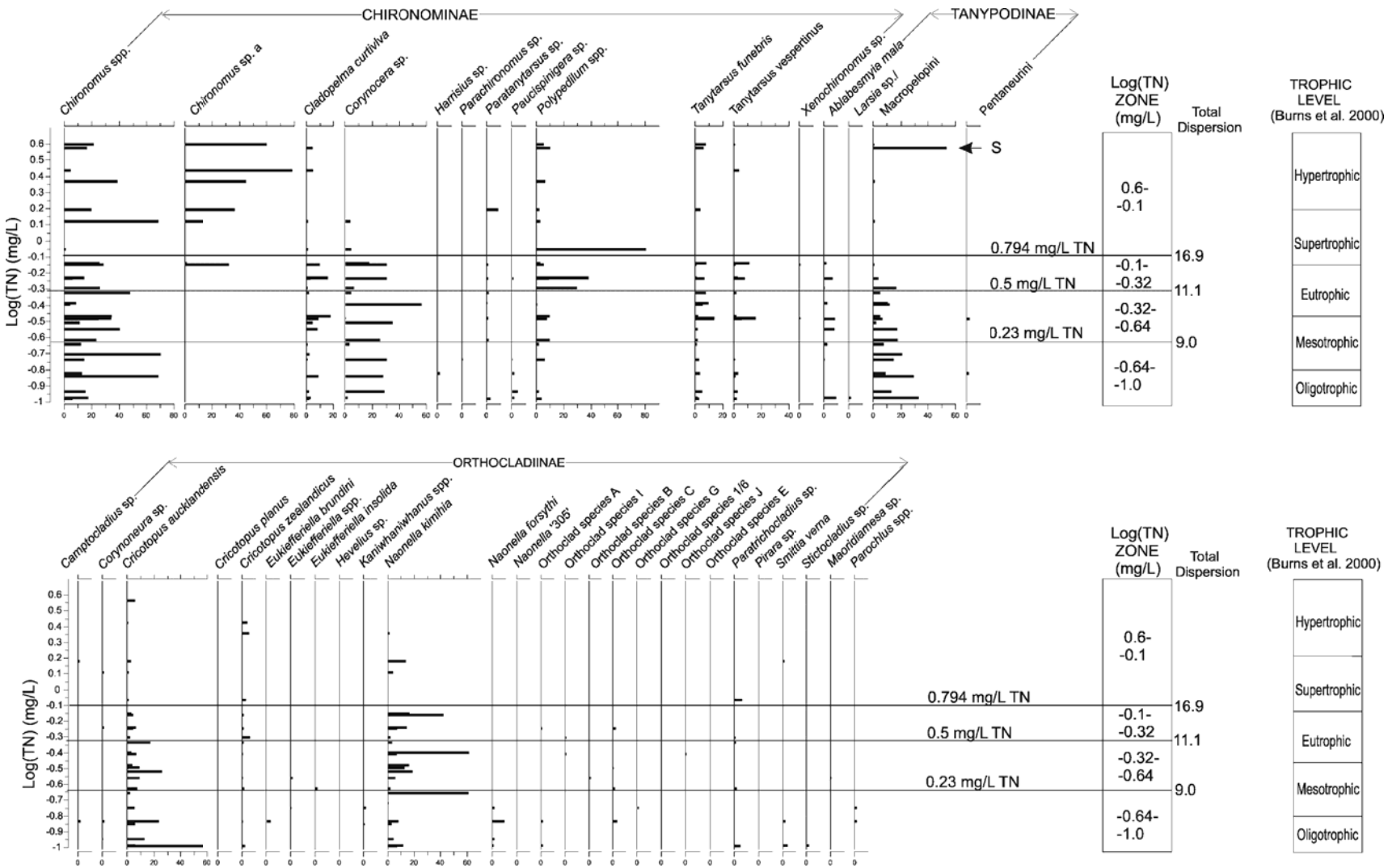


Fig. 5.20: Chironomid relative abundances for the productivity training set including all 43 taxa with respect to the TN gradient. X axis = relative abundance (%). Total dispersion values are provided based on constrained incremental sum of sqaures (CONISS) in Zone 1.2. It is important to note that the trophic definitions of Burns et al. (2000) are based on annual average TN values. The position of Swan Lagoon (S) is also indicated.

More abundant macrophyte growth in mesotrophic lakes could result in an increased abundance of this taxon. *Polypedilum* spp. also seems to be more abundant in mesotrophic to eutrophic lakes, but disappears in hypertrophic lakes. Previous studies from elsewhere in the world have shown increased abundances of Polypedilum in response to moderate increases in trophic status (e.g. Warwick, 1975; Brodin, 1982; Hall et al., 1999). *Chironomus* spp. and *Chironomus* sp. a were the only common chironomid taxa in the hypertrophic New Zealand lakes in this training set. Chironomus has also been observed to be typical of eutrophic conditions in chironomid training sets from other parts of the world (e.g. Brooks et al., 2001)

5.3 CONCLUSIONS

Air temperature (February mean) and lake primary production (chlorophyll *a*) emerged as the variables that explained the largest unique amount of variance in the taxonomic data from the entire training set. Conductivity and the concentration of total phosphorus (TP) were also significant determinants of chironomid taxonomic variance. Temperature appeared to have the largest conditional effect (7.0%) on the chironomid taxonomic variance after the effects of all the other environmental variables were partialled out. It was not possible to use any of the environmental parameters from the entire training set for transfer function development as there is a high degree of colinearity between the environmental gradients. The effects of the environmental parameters on the chironomid taxonomic variance were also confounded.

It was therefore necessary to subdivide the training set into two subsets: the temperature training set (n = 32) and a productivity/chemistry training set (n = 32). All sites with significant proportions of agriculture or populated areas were removed from the temperature training set, while all sites with February mean air temperature below 12ºC were removed from the productivity/chemistry training set.

February mean temperature explained the largest (8.0%) unique, significant (P = 0.001) proportion of the chironomid taxonomic variance in this dataset, and is therefore the variable that is most suitable for transfer function development. The February mean temperature for this dataset ranged from 8ºC in high altitude (ca. 2000m) lakes to 16.8 ºC in lowland (435m) lakes. Lake production (chlorophyll *a*) and the concentration of dissolved reactive phosphorus (DRP) were also included as a constraining environmental variables in the final CCA but they explained a smaller and less significant proportion of the toal taxonomic variance. The effects of chlorophyll *a* and DRP were confounded, but seem to represent a weak secondary trophic gradient in the temperature

training set. Water depth and the percentage of ice and snow in the catchment were also included as constraining variables in the final CCA plot. Even though the effect of these variables was small and not significant ($P< 0.01$) compared to air temperature, it appears that these variables do contribute somewhat to the taxonomic variance in the high altitude lakes where many of the chironomid taxa are near their temperature tolerance limits. Increasing lake depth and the input of melt-water results in lower lake-water temperatures, and a differential between water and air temperatures. Despite some deeper lakes and lakes with snow-melt input being included in this training set, February mean air temperature still explained a relatively high, significant amount of the total taxonomic variance. A total of 34.5% of the chironomid taxonomic variance was explained by these five variables.

Electrical conductivity of the lake water appeared to explain the largest amount of the taxonomic variance in the productivity/chemistry training set. Both conductivity and the concentration of total nitrogen (TN) were highly correlated to CCA axis 1. It appears that the effect of conductivity is actually an illusion created by the high degree of correlation between conductivity and the trophic variables (TN, total phosphorus (TP), and chlorophyll *a* (Chla)). Examination of previous studies along salinity gradient s for the New Zealand chironomid genus Chironomus, and comparison of equivalent taxonomic groups from elsewhere in the world confirm that conductivities below 400 µS/cm are too low to actually be a true limiting factor.

TN was therefore selected as the trophic variables that explained the largest (5.0%) significant proportion of the chironomid variance and is therefore the variable that is most suitable for transfer function development.

Now that two environmental parameters have been selected (February mean air temperature and TN) transfer functions will be developed for these variables in the following section.

CHAPTER 6: THE DEVELOPMENT OF CHIRONOMID-BASED INFERENCE MODELS FOR PALEOENVIRONMENTAL RECONSTRUCTIONS

PART III: MODEL DEVELOPMENT. RESULTS & DISCUSSION

6.1 RESULTS

6.1.1 Transfer function development

The results of the exploratory data analyses outlined in the previous chapter indicate that February mean temperature (Feb Mean) and total phosphorus (TP) are the most suitable environmental variables for the development of chironomid-based inference models. The methodology for model development and assessment was outlined in **Chapter 4**, **Section 4.4.4**. Even though the results of separate detrended canonical correspondence analyses (DCCAs) (constrained to Feb Mean and TP respectively) revealed short gradient lengths for for DCCA axis 1 (**Table 6.1** and **6.2**), both linear (partial least squares (PLS)) and unimodal (e.g. weighted averaging – partial least squares (WA-PLS)) techniques were tested. ter Braak and Prentice (1988) state that when gradient lengths are short (< 2 standard deviations (SD)) linear-based methods should be more appropriate for inference model development. However, ter Braak et al. (1993) have shown using simulated and real data that models based on unimodal techniques often out-perform those based on linear techniques (higher r^2, lower root mean squared error of prediction (RMSEP)) when the gradient length is short.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.147	0.153	0.071	0.05	1.028
Lengths of gradient :	**1.415**	1.646	1.479	1.027	
Species-environment correlations :	0.832	0	0	0	
Cumulative percentage variance					
of species data :	14.3	29.2	36.1	41	
of species-environment relation:	100.8	99.4	0	0	
Sum of all eigenvalues					1.028
Sum of all canonical eigenvalues					0.147

Table 6.1: Results of a partial DCCA Constrained to February mean temperature for the temperature training set (n = 31). The gradient length is short for DCCA axis 1 (1.415), which suggests that linear methods should be more appropriate for the development of a chironomid-based inference model.

Axes	1	2	3	4	Total inertia
Eigenvalues :	0.244	0.103	0.073	0.035	1.091
Lengths of gradient :	**1.713**	1.772	1.224	1.602	
Species-environment correlations :	0.913	0	0	0	
Cumulative percentage variance					
of species data :	22.4	31.8	38.5	41.7	
of species-environment relation:	76.4	77.4	0	0	
Sum of all eigenvalues					1.091
Sum of all canonical eigenvalues					0.244

Table 6.2: Results of a partial DCCA constrained to TN for the productivity/chemistry training set (n = 32). The gradient length for DCCA axis 1 is short (1.713) which suggests that linear methods should be most suitable for developing a chironomid-based inference model for this variable.

February mean model performance:

The performance statistics for the February mean temperature inference models are provided in **Table 6.3**: **1**, **A**, **B**, and **C**. Extra components were only included for PLS and WA-PLS if the new model reduced the RMSEP by at least 5% (Birks, 1998). For both PLS and WA-PLS a model with 2 components was identified as the minimum adequate model. The performance of the unimodal (WA and WA-PLS) and linear (PLS) based models were similar, with and r^2_{jack} of 0.738, 0.702, and 0.660 and a RMSEP of 1.28, 1.34, and 1.43 °C respectively. The WA model with tolerance down-weighted and classical deshrinking performed slightly better than the WA models based on inverse deshrinking. The best unimodal-based models (WA and WA-PLS) had higher coefficients of determiniation (r^2_{jack}) and lower RMSEP than the linear based models. However the model based on PLS with 2 components had a lower cross-validated (jack-knifed) maximum and average bias (1.64 and -.013°C respectively). Plots of predicted vs observed and residual plots for the WA-PLS, WA, and PLS based transfer functions are depicted in **Fig. 6.1A, B,** and **C** respectively. All models have a tendency to over-predict cooler temperatures and under-predict warmer temperatures. The discrepancy between the observed and predicted Feb Mean temperatures for the WA-PLS model is greatest for Little Sylvester Lake and "Avon", which are over-predicted, and Lake Mistletoe and Lake Pearson, which are under-predicted (**Fig. 6.1A**). In the case of the WA model, the Feb Mean temperatures for "Rainbow West" and Lake Roundabout were most severely over-predicted, while the Feb Mean temperatures for Lake Mackenzie and Lake Rerewhakaaitu were most severely under-predicted (**Fig. 6.1B**). The Feb Mean temperatures for Little Sylvester Lake and "Sugarbowl Tarn" were most severely over-predicted using the PLS-based model, while Lake Pearson and Sylvan were most severely under-predicted. The largest discrepancy between the observed and predicted

1 FEBRUARY MEAN MODEL PERFORMANCE RESULTS

A. Weighted averaging - Partial least squares

#	Code	Name	r^2	Ave_Bias	Max_Bias	Jack_r^2	Jack_Ave_Bias	Jack_Max_Bias	RMSEP	%Change
1	Component 1	WAPLS Component 1 for Feb Mean	0.758	-0.068	1.794	0.628	-0.167	2.264	1.505	...
2	**Component 2**	**WAPLS Component 2 for Feb Mean**	**0.865**	**0.007**	**1.261**	**0.702**	**-0.089**	**1.773**	**1.336**	**11.183**
3	Component 3	WAPLS Component 3 for Feb Mean	0.890	0.010	1.466	0.663	-0.041	2.252	1.452	-8.630
4	Component 4	WAPLS Component 4 for Feb Mean	0.903	0.012	1.401	0.639	-0.048	2.419	1.510	-4.024
5	Component 5	WAPLS Component 5 for Feb Mean	0.919	-0.007	0.715	0.617	-0.032	2.136	1.589	-5.193

B. Weighted averaging

#	Code	Name	r^2	Ave_Bias	Max_Bias	Jack_r^2	Jack_Ave_Bias	Jack_Max_Bias	RMSEP
1	WA_Inv	Weighted averaging model (inverse deshrinking) for Feb Mean	0.758	2.768E-14	1.827	0.630	-0.102	2.296	1.492
2	WA_Cla	Weighted averaging model (classical deshrinking) for Feb Mean	0.758	2.985E-14	1.222	0.644	-0.124	1.675	1.541
3	WATOL_Inv	Weighted averaging model (tolerance downweighted, inverse deshrinking) for Feb Mean	0.829	-1.891E-15	2.127	0.732	-0.179	2.285	1.293
4	**WATOL_Cla**	**Weighted averaging model (tolerance downweighted, classical deshrinking) for Feb Mean**	**0.829**	**-6.762E-15**	**1.725**	**0.738**	**-0.204**	**1.965**	**1.283**

C. Partial least squares

#	Code	Name	r^2	Ave_Bias	Max_Bias	Jack_r^2	Jack_Ave_Bias	Jack_Max_Bias	RMSEP	%Change
1	Component 1	PLS Component 1 for Feb Mean	0.709	-1.146E-15	2.062	0.571	-0.020	2.686	1.601	...
2	**Component 2**	**PLS Component 2 for Feb Mean**	**0.814**	**-9.741E-16**	**1.298**	**0.660**	**-0.013**	**1.639**	**1.425**	**11.034**
3	Component 3	PLS Component 3 for Feb Mean	0.843	-1.031E-15	1.841	0.666	0.007	2.357	1.418	0.450
4	Component 4	PLS Component 4 for Feb Mean	0.862	-1.031E-15	1.637	0.645	-0.005	2.455	1.480	-4.348
5	Component 5	PLS Component 5 for Feb Mean	0.874	-1.089E-15	1.355	0.617	-0.079	2.448	1.572	-6.243

2 TN MODEL PERFORMANCE RESULTS

A. Weighted averaging - Partial least squares

#	Code	Name	r^2	Ave_Bias	Max_Bias	Jack r^2	Jack_Ave_Bias	Jack_Max_Bias	RMSEP	%Change
1	Component 1	WAPLS Component 1 for TN	0.821	-0.0046	0.221	0.763	-0.0041	0.263	0.195	...
2	**Component 2**	**WAPLS Component 2 for TN**	**0.887**	**-0.0001**	**0.257**	**0.800**	**0.0008**	**0.327**	**0.179**	**7.931**
3	Component 3	WAPLS Component 3 for TN	0.905	0.0011	0.234	0.791	0.0003	0.318	0.188	-4.713
4	Component 4	WAPLS Component 4 for TN	0.918	0.0011	0.233	0.776	0.0072	0.369	0.204	-8.574
5	Component 5	WAPLS Component 5 for TN	0.925	0.0006	0.240	0.753	0.0164	0.393	0.224	-9.734

B. Weighted averaging

#	Code	Name	r^2	Ave_Bias	Max_Bias	Jack_r^2	Jack_Ave_Bias	Jack_Max_Bias	RMSEP
1	**WA_Inv**	**Weighted averaging model (inverse deshrinking) for TN**	**0.821**	**-6.20E-17**	**0.220**	**0.761**	**0.0003**	**0.262**	**0.195**
2	WA_Cla	Weighted averaging model (classical deshrinking) for TN	0.821	-2.31E-17	0.353	0.767	-0.0030	0.391	0.210
3	WATOL_Inv	Weighted averaging model (tolerance downweighted, inverse deshrinking) for TN	0.816	-1.40E-16	0.223	0.712	0.0038	0.281	0.214
4	WATOL_Cla	Weighted averaging model (tolerance downweighted, classical deshrinking) for TN	0.816	-5.27E-17	0.344	0.722	0.0015	0.339	0.228

C. Partial least squares

#	Code	Name	r^2	Ave_Bias	Max_Bias	Jack_r^2	Jack_Ave_Bias	Jack_Max_Bias	RMSEP	%Change
1	Component 1	PLS Component 1 for TN	0.818	-8.23E-17	0.227	0.761	0.000	0.285	0.196	...
2	**Component 2**	**PLS Component 2 for TN**	**0.881**	**-1.01E-16**	**0.225**	**0.786**	**0.006**	**0.287**	**0.185**	**5.416**
3	Component 3	PLS Component 3 for TN	0.907	-9.16E-17	0.196	0.800	-0.005	0.296	0.181	2.616
4	Component 4	PLS Component 4 for TN	0.920	-9.34E-17	0.209	0.805	0.001	0.328	0.178	1.467
5	Component 5	PLS Component 5 for TN	0.930	-9.34E-17	0.206	0.813	0.005	0.333	0.176	1.046

Table 6.3: **1.** Model results from February mean inference models. **2**. Model results from TN inference models. Row that is emphasised in bold is the best model for each method. Ave_Bias = Average bias; Max_Bias = maximum bias; Jack r2 = jack-knifed r2; Jack_Ave_Bias = jack-knifed average bias; Jack_Max_Bias = jacknifed maxium bias; RMSEP = Root mean squared error of prediction; % Change = % improvement of error on previous component
The very small values in the avergae bias column (Ave-Bias) are represented in the format for scientific notation produced in Microsoft® EXCEL e.g., 2.07E-16 = 2.07×10^{-16}

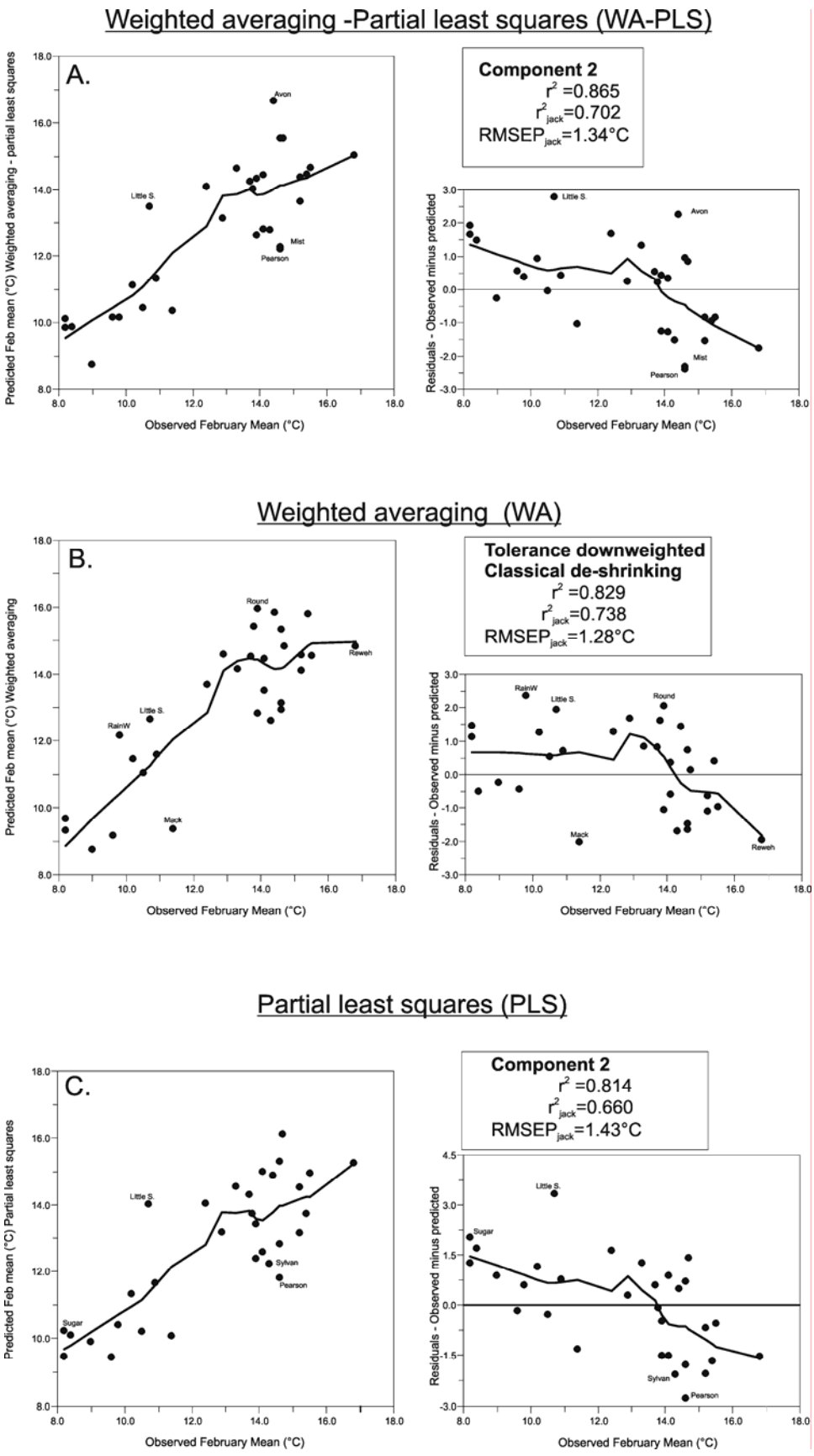


Fig. 6.1: Plots of predicted vs observed and residuals for February mean transfer functions produced in C2 (Juggins, 2003).
In each plot a LOWESS smoother has been fitted with a span of 0.45. Several data-points have been labelled with lake names. The abbreviations for these lakes are provided in **Table 5.2**.

Feb Mean temperatures was produced by the PLS model. The Feb Mean temperature for Little Sylvester Lake was over-predicted by over 3 °C.

Total nitrogen (TN) model performance:

Plots of observed vs inferred Log (TN) and residuals for an initial WA (inverse de-shrinking) inference model are depicted in **Fig. 6.2**. One lake (Swan Lagoon) is an obvious outlier, with the Log(TN) concentration severely under-predicted. There is good reason to remove this lake from the final model. This lake contained a high abundance (ca 50%) of head-capsules belonging to the tribe Macropelopini. Head-capsules belonging to this group are typical of oligotrophic to mesotrophic lakes. This is the only lake with Log(TN) concentrations above -0.1 mg/L to have such a high abundance of head-capsules belonging to this group (**Fig. 5.20**). The fact that TN concentrations are derived from spot samples taken during a single summer means that the lake conditions during sampling may not be truly representative of the average conditions in each lake. Swan Lagoon appears to represent an extreme example of this discrepancy. Swan Lagoon was particularly shallow (1.4m) and turbid at the time of sampling. Water marks and large drifts of dead aquatic weed indicate that the water levels were recently at least 40 cm higher **(Fig. 6.3**). The chironomid fauna is more typical of a clear oligotrophic lake. Lowering of the lake levels would have exposed the macrophyte beds to wind disturbance resulting in their destruction. Loss of the macrophyte beds would have de-stabilised the sediments resulting in an increase in turbidity, and possibly re-suspending nutrients stored in the sediments.

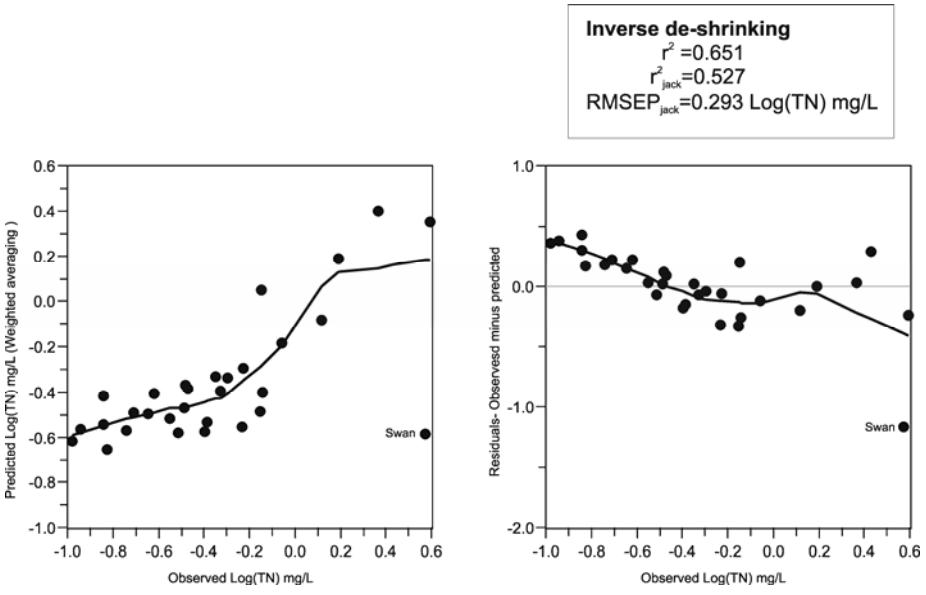


Fig. 6.2: Plots of predicted vs observed and residuals for a WA TN transfer function produced in C2 (Juggins, 2003).
In each plot a lowess smoother has been fitted with a span of 0.45. The location of Swan Lagoon has been identified. The water level for Swan Lagoon was particularly low at the time of sampling and may not represent typical conditions.

Hamilton and Mitchell (1997) have demonstrated that wind shear is responsible for exclusion of macrophytes from the benthos of New Zealand shallow lakes and the triggering of blooms of planktonic algae. Swan Lagoon was quite exposed (**Fig 6.3**) and the north-west winds on the eastern side of the Southern Alps can reach speeds of up to 180 km/h (McGowan et al., 2002). Swan Lagoon was therefore removed from the training set for the final inference models.

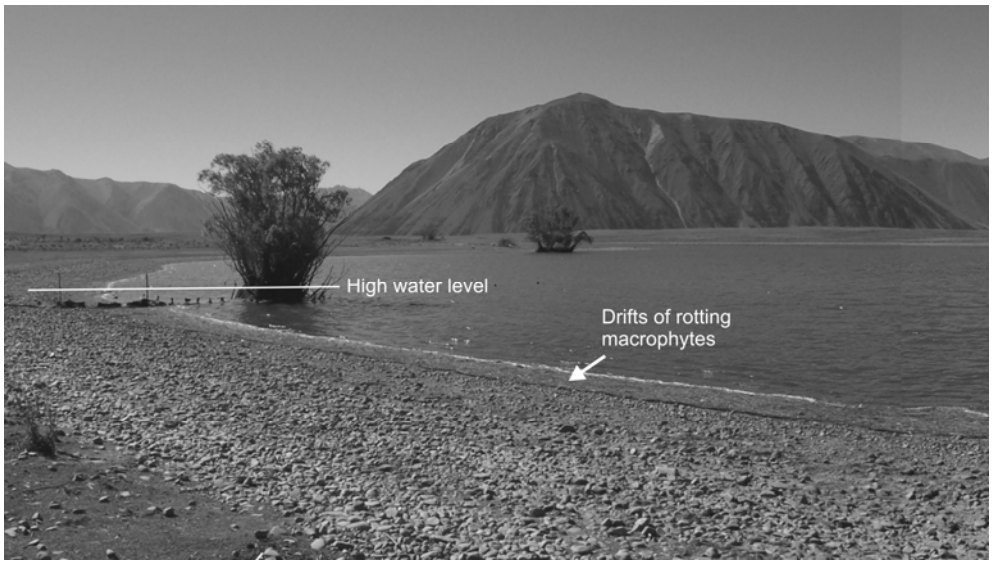


Fig. 6.3: Swan Lagoon near Lake Ohau, lake 36 in Fig. 4.2 and Table 4.1. The chironomid assemblage from this lake is more typical of an oligotrophic clear lake. The lake is currently shallow, turbid and eutrophic with no living macrophytes. Drifts of rotting macrophytes and evidence for higher water-levels suggest the possibility that this lake was oligotrophic-mesotrophic with abundant macrophytes and clear water.

The resulting inference models (**Table 6.3**, **Fig. 6.4**) were far more robust, with a reduction of the RMSEP of approximately 25%. The WA-PLS and PLS based models were more robust than the WA based model. The WA-PLS based model performed slightly better than the PLS based model. The WA-PLS model had the highest r^2, lowest RMSEP, and lowest average bias. The WA model had a slightly lower maximum bias than the WA-PLS model (**Table 6.3**). The distribution of the residuals is more random along the TN gradient in the case of the WA-PLS and PLS models than the WA model. The coefficient of variation for the WA-PLS, PLS, and WA based models was determined in Microsoft® Office Excel. The r^2 for each model was 0.134, 0.169, and 0.230 for the WA-PLS, PLS and WA-based models respectively. There is an obvious trend towards over-prediction of the TN concentration with the WA-based TN model at the low end of the TN gradient (**Fig.6.4**). For the WA-PLS and PLS models there is a tendency towards over-prediction and under-prediction of the TN concentration at the low and high end of the TN gradient respectively. This effect is more pronounced for the PLS based model.

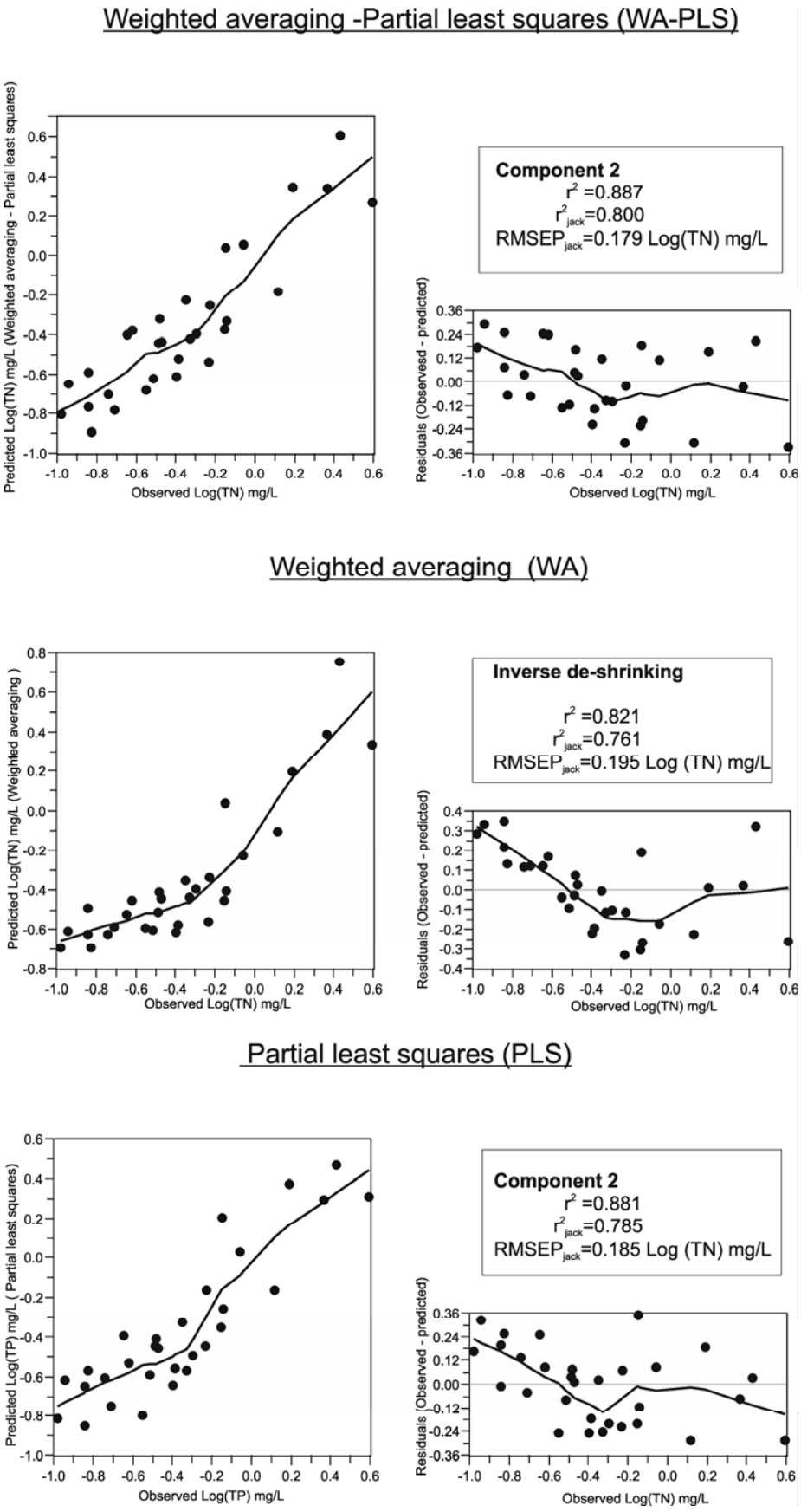


Fig. 6.4: Plots of predicted vs observed and residuals for TN transfer functions produced in C2 (Juggins, 2003).
In each plot a LOWESS smoother has been fitted with a span of 0.45. Several data-points have been labelled with lake names. The abbreviations for these lakes are provided in **Table 5.2**

6.1.2 Taxon response models

February mean air temperature taxon response models:

9 out of the 17 taxa (53%) used in the February mean temperature inference models show statistically significant relationships to the February mean temperature gradient (**Table 6.4** and **Fig. 6.3**). This figure does not include *Coynocera* sp.. The resulting model for this taxon was significant (P =0.001) but is technically a null model as the fitted curve is a horizontal line (**Fig. 6.5**). Of the 9 taxa that displayed a significant response to February mean temperature, 3 (*Cricotopus aucklandensis, Cricotopus zealandicus,* and *Paratanytarsus grimmii*) displayed a unimodal (quadratic, Poisson distribution) response to temperature. The other 6 taxa displayed a sigmoidal linear (linear, Poisson distribution) response to temperature. *Cladopelma curtivalva* and *Parochlus* spp. displayed the most significant response to February mean temperature (P = 0.00009 and 0.00075 respectively). The response of *Chironomus* spp. is also depicted in **Fig. 6.5**, but the significance (P- value) of the linear model was greater than 0.05.

Species	Model	F	P	Optimum	Tolerance
Ablabesmyia mala	QP	1.59	0.221	13.7	2.53
Chironomus spp.	QP	2.12	0.139	ce	ce
	LP	3.01	0.093	NA	NA
Cladopelma curtivalva	QP	9.96	0.0005	40.99	6.8
	LP	20.37	0.00009	NA	NA
Corynocera sp.	QP	2.42	0.106	12.15	1.75
	LP	0.00	0.001	NA	NA
Cricotopus aucklandensis	QP	11.89	0.00018	14.66	1.99
	LP	13.87	0.0008	NA	NA
Cricotopus zealandicus	QP	5.78	0.0078	14.6	0.867
	LP				
Macropopelopini	QP	1.34	0.27	12.72	3.14
Naonella forsythi	QP	2.87	0.07	ce	ce
	LP	4.77	0.037	NA	NA
Naonella kimihia	QP	3.82	0.034	17.63	3.87
Orthoclad species C	QP	0.12	0.111	ce	ce
Paratanytarsus grimmii	QP	6.11	0.006	15.41	1.15
Parochlus spp.	QP	6.85	0.0037	ce	ce
	LP	14.19	0.00075	NA	NA
Paucispinigera sp.	QP	1.12	0.34	12.65	1.98
Polypedilum spp.	QP	3.38	0.048	21.51	4.41
	LP	6.62	0.0154	NA	NA
Smittia verna	QP	0.12	0.114	11.23	3.41
Tanytarsus funebris	QP	1.39	0.265	10.44	3.44
Tanytarsus vespertinus	QP	6.17	0.006	ce	ce
	LP	12.63	0.001	NA	NA

Table 6.4: Results of generlaised linear model (GLM) testing in CANOCO 4.5. for individual taxa with respect to the February mean temperature gradient. Models that **are** significant (P < 0.05) are highlighted with grey. NA = not applicable (i.e. no estimates of optima or tolerances for linear methods) ce = cannot estimate. QP = unimodal model (Quadratic Poisson), LP = sigmoidal linear (Linear Poisson).

Taxon	Model	F	P	Opt	Tol
Ablabesmyia mala	LP	2.56	0.1209	NA	NA
Chironomus spp.	LP	0.155	0.303	NA	NA
Chironomus sp. a	LP	73.74	<0.000001	NA	NA
Cladopelma curtivlava	QP	1.13	0.338	-0.395	0.497
Corynocera sp.	QP	2.18	0.133	-0.516	0.417
Cricotopus aucklandensis	LP	7.72	0.009	NA	NA
Cricotopus zealandicus	LP	5.26	0.029	NA	NA
Macropelopini	LP	49.57	<0.000001	NA	NA
Naonella forsythi	LP	15.59	0.0005	NA	NA
Naonella kimihia	QP	2.34	0.116	-0.385	0.373
Orthoclad species C	LP	1.87	0.182		
Paratrichocladius pluriserialis	QP	1.78	0.187	-0.116	0.249
Paratanytarsus grimmii	QP	2.19	0.121	0.102	0.381
Polypedilum spp.	QP	4.83	0.016	-0.055	0.296
Smittia verna	QP	3.32	0.051	ce	ce
Tanytarsus funebris	LP	0.003	0.039	NA	NA
Tanytarsus vespertimus	LP	0.005	0.058	NA	NA

Table 6.5: Results of generalised linear model (GLM) testing in CANOCO 4.5. for individual taxa with respect to the total nitrogen (TN) gradient. Models that **are** significant ($P < 0.05$) are highlighted with grey. NA = not applicable (i.e. no estimates of optima or tolerances for linear methods) ce = cannot estimate. QP = unimodal model (Quadratic Poisson), LP = sigmoidal linear (Linear Poisson).

Total Nitrogen taxon response models:

Only 6 of the 17 taxa (35%) used in the total nitrogen (TN) models displayed a significant response to the TN gradient. This does not include *Tanytarsus funebris*, the model fitted to this taxon equates to a null model (a horizontal line) with a significance of 0.039. A linear model had the most significant fit for the abundance data of five out of the six significant taxa (**Table 6.5**, **Fig. 6.6**). The significance of the relationship between species abundance and Log(TN) concentration was highest for *Chironomus* sp. a and the Macropelopini ($P < 0.000001$). The abundance of *Chironomus* sp. a was positively correlated with the Log(TN) concentration while the abundance of the Macropelopini was negatively correlated to the Log(TN) concentration. *Cricotopus zealandicus* was the only other taxon with a positive linear correlation to the Log(TN) concentration. *Polypedilum* spp. was the only taxon for which the unimodal model had a more significant fit to the taxon abundance data than a linear model. The optimum for *Polypedilum* spp. as calculated in CANOCO 4.5 was -0.055 Log(TN) mg/L. This equates to a summer TN concentration of ca. 0.8 mg/L.

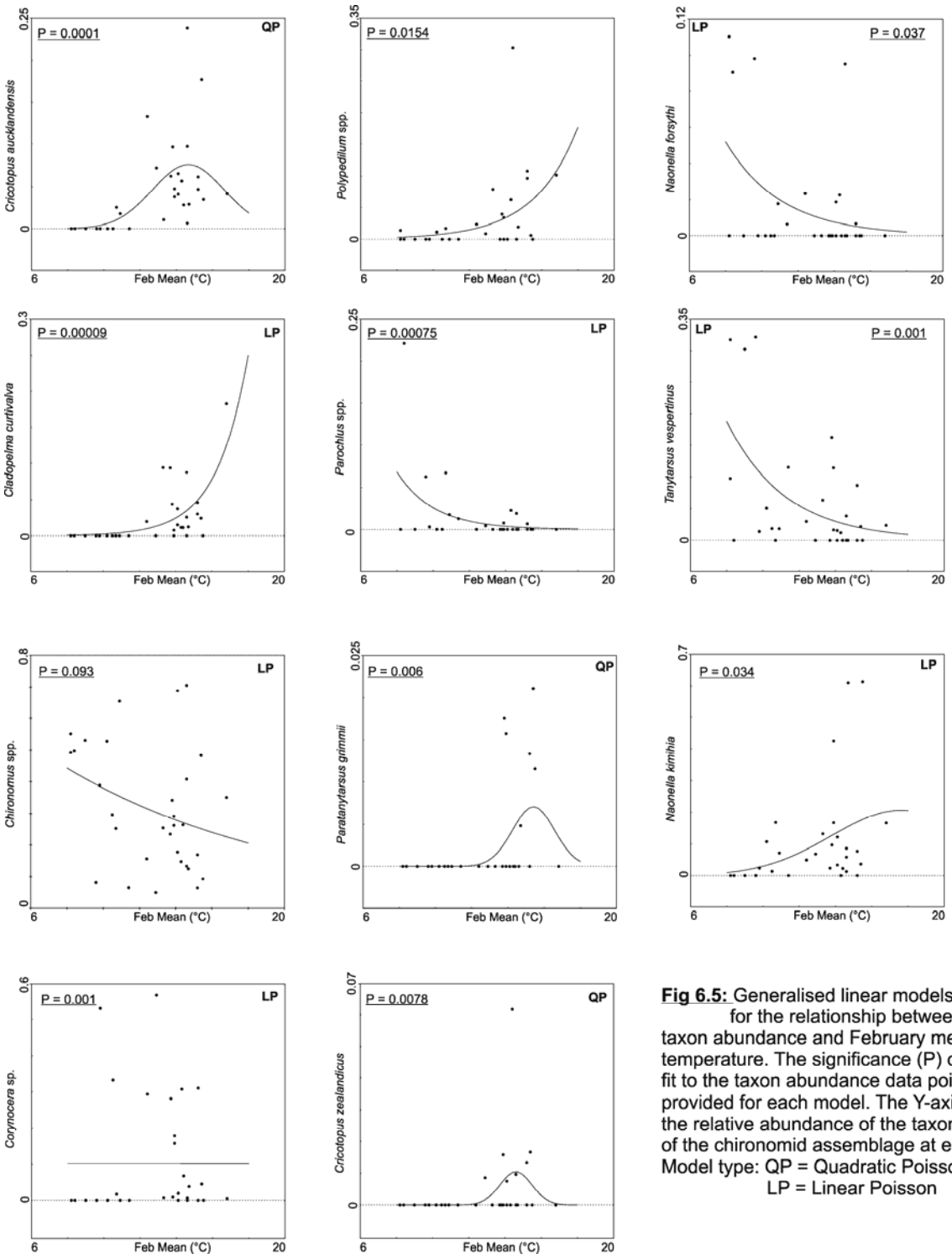


Fig 6.5: Generalised linear models (GLMs) for the relationship between relative taxon abundance and February mean temperature. The significance (P) of the model fit to the taxon abundance data points is provided for each model. The Y-axis represents the relative abundance of the taxon as a proportion of the chironomid assemblage at each site.
Model type: QP = Quadratic Poisson (unimodal)
LP = Linear Poisson

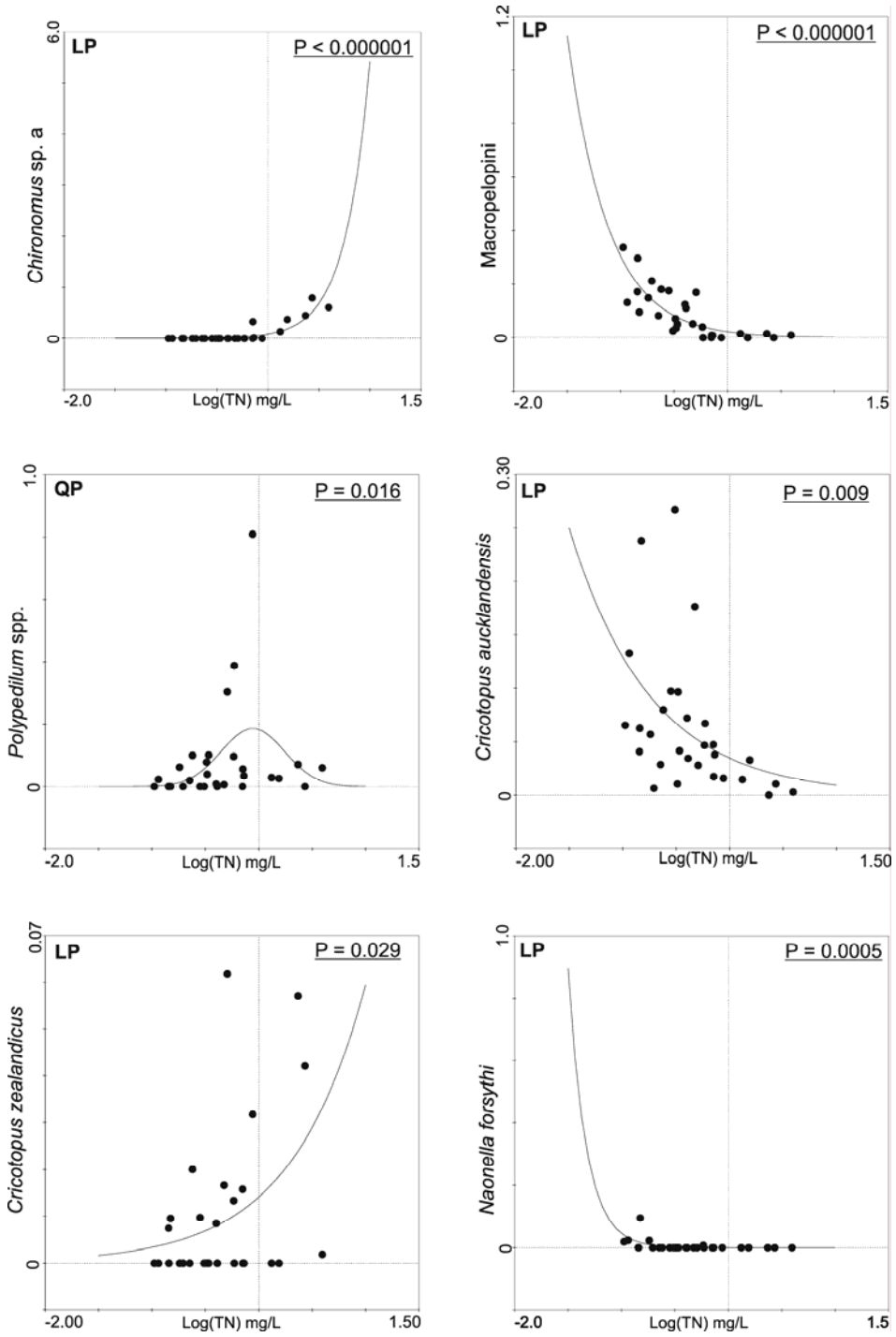


Fig. 6.6: Generalised linear models (GLMs) for the relationship between taxon abundance and Log(TN) for the 6 taxa with a significant (P <0.01) relationship to TN. The significance of the fit of each model is provided. The y-axis represents taxon abundance as a proportion of the total head-capsule count at each site. LP = linear Poisson, QP = Quadratic Poisson (Unimodal).

6.2 DISCUSSION

6.2.1 Transfer function performance and taxon response

February mean:

The transfer-functions resulting from WA-PLS, WA, and PLS were all relatively robust. An assessment of the performance of a transfer-function is based on the r^2, average bias, maximum bias, and the RMSEP. The best model from each technique (unimodal vs linear) performed better than the others for some of these criteria, but there was no individual model that outperformed the others for all of these criteria. The WA (tolerance down-weighted) model had the highest r^2 and the lowest RMSEP, but also had the highest maximum and average bias. The PLS model with (2 components) had the lowest maximum and average bias, but had the highest RMSEP and lowest r^2 (**Table 6.3, Fig. 6.1**). Birks (1998) suggested that the selection of the final model should be determined by the subsequent application of the models and the research questions being addressed. One of the main questions to be addressed by this my research concerns the degree of cooling during the last glacial. As the main target is the maximum amount of cooling, it would preferable to use a model with a low mean and average bias at the low end of the temperature gradient (< 12 ºC). For this purpose, the tolerance downweighted, weighted averaging model seems most appropriate. This model has a low RMSEP, a high r^2, and the fitted LOWESS smoother indicates that there isn't a trend in the residuals at the low end of the temperature gradient. The maxium bias for the WA model is less than 2.5 ºC. The WA-PLS model and the PLS model have a maximum bias that is greater than 2.5 ºC and there is an obvious trend towards over-prediction at the lower end of the temperature gradient. All three models have the tendency to under-predict temperatures at the high end of the temperature gradient (**Fig. 6.1**).

The resulting transfer functions appear to be robust, despite the fact that only 17 out of the 31 taxa (52.9%) included in the final models had a significant ($P < 0.05$) response to temperature (**Table 6.8**). I would expect that taxa that did not have a significant response to February mean would introduce noise into the resulting models. Studies involving other proxies (e.g. diatoms (Racca et al., 2004)) have shown that removal of taxa that do not show a significant response to the target variable may increase the performance of the resulting transfer- function. In this study, removal of taxa that were scarce (not present >2% in at least 2 lakes) did improve the transfer function performance

(**Table 6.6**). Removal of the more common taxa (>2% in at least 2 lakes) that did not show a significant response to February mean temperature (**Table 6.4**) did not improve the model performance (**Table 6.6**). The r^2 decreased for the WA-PLS model from 0.7 to 0.64, and the RMSEP increased from 1.34 to 1.49 ^oC. In terms of the RMSEP, the addition of the non-significant taxa improves the model performance by > 5%, which is a suggested criterion for the acceptance of a minimal adequate model (Birks, 1998).

Other studies that have developed chironomid-based temperature transfer-functions have shown that robust models can be developed even though only a fraction of the taxa show a significant response (**Table 6.7**). Laroque et al. (2001) found that 69.8% of the 42 taxa included in the final July mean air temperature model displayed a significant response to temperature. Interestingly, even though a higher proportion of the taxa displayed a significant response in the Laroque et al. (2001) training set, the r^2 was lower and the maximum bias higher than the model that resulted from this study. Lotter et al. (1999) found that 88% of the 57 taxa used in their final July mean air temperature model displayed a significant response. The r^2 was higher than this study (0.81), but the absolute RMSEP and maxium bias were higher. Both of these studies have more than twice the number of taxa included in their final temperature models (i.e. 42 and 57 taxa respectively) than were included in the final model in my thesis. The limited amount of data available here indicates that this does not necessarily result in a more robust inference model as assessed by all performance criteria (r^2, maximum and average bias).

Three of the most common taxa (*Chironomus* spp., *Corynocera* sp. and Macropelopini) did not show a significant response to February mean temperature in this thesis (**Table 6.4**, **Fig. 6.5**). This could mean that some other variable is the primary controlling factor for these taxa. I believe that there are several other reasons for the poor explanatory power of temperature for these taxa. The taxonomic resolution for these taxa is certainly a factor. This is particularly the case with *Chironomus* spp.. This taxon is likely to represent 7 *Chironomus* species, but at this stage it is not possible to separate these species by head-capsule morphology alone (see **Chapter 2**). General observations made during the course of this study lead me to believe that the high altitude fauna are dominated by *Chironomus* sp. 8. Low altitude oligotrophic-mesotrophic lakes appeared to be dominated by *Chironomus novae-zelandiae*. This speculation was based on the examination of live material collected during visits to each of the lakes. The pigmentation of the gular region for these species is quite different. *Chironomus* sp. 8. has little or no pigmentation, while the bottom half of the gular region is strongly pigmented in *Chironomus novae-zealandiae* (**Fig. 2.11a** and **b**

respectively, **Chapter 2**). Unfortunately this feature is unlikely to be preserved in the fossil record, particularly with older (> 10,000 years) samples.

As *Chironomus* spp. is the most common morphotype, it is likely to be a source of error in the temperature transfer-function. The best fitted model for the *Chironomus* spp. morphotype was a linear model with a significance of P = 0.093 (**Fig. 6.4** and **6.7**). There was a weak negative correlation, with *Chironomus* spp. being more common in the high altitude (colder) sites. The temperature optimum for *Chironomus* spp. was calculated in C2 (Juggins, 2003) using weighted averaging (WA). The temperature optimum was ~ 12.5 ºC (**Fig. 6.7**). This suggests that a high abundance of *Chironomus* spp. may lead to an over-prediction of cooler temperatures and an under prediction of warmer temperatures using the WA model where *Chironomus* spp. is abundant. This was the case for Lake Pearson (a lowland lake) and several of the high altitude lakes (e.g. Sugarbowl Tarn) that had high abundances of *Chironomus* spp.. The main effect of *Chironomus* spp. in the WA-PLS model is likely to be an under-prediction of the warmer temperatures where *Chironomus* spp. is common. The beta coefficient for *Chironomus* spp. was ~ 8.5ºC (**Fig. 6.7**). The February mean air temperatures for both Lake Taylor and Pearson (which both have high abundances of *C.* spp. (**Fig. 6.7**) where under-predicted by 1.5 and 2 ºC respectively.

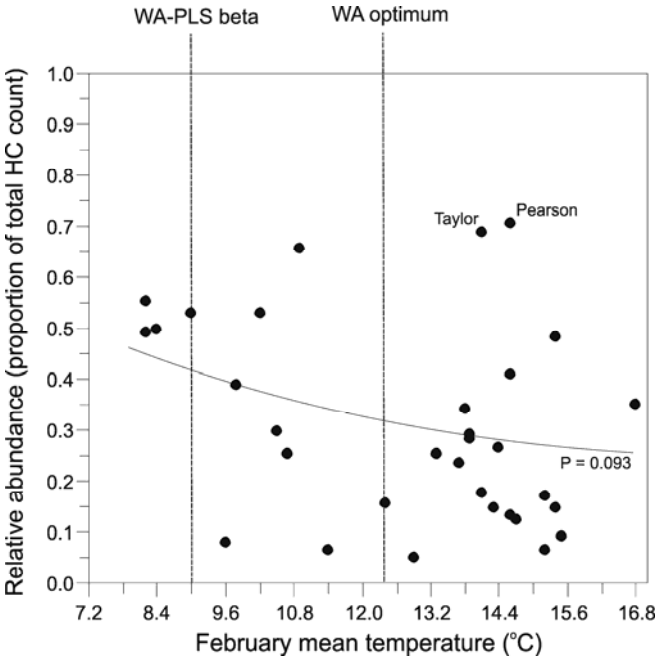


Fig. 6.7: The relative abundance of the *Chironomus* spp. morphotype with respect to temperature. The best fitted GLM (linear sigmoidal) is shown, as well as the optimum calculated by weighted averaging (WA optimum). The beta-coffecient from the WA-PLS is also shown (WA-PLS beta). This data suggests that temperature predictions using the WA model from sites with a high abundance of *Chioronomus* spp. (such as Taylor and Pearson) will be under-predicted, while high altitude lakes with a high abundance of *Chironomus* spp. will be over-predicted. The WA-PLS beta coefficient is low (~ 8.5 °C). This suggests that the main effect of *Chironomus* spp. in WA-PLS models would be to cause an under-prediction of warmer temperatures in lakes with a high percentage of *Chironomus* spp.

Efforts were made to sample lakes that were evenly distributed along the temperature gradient. Unfortunately the resulting data set is deficient in lakes in part of the temperature gradient. There is a distinct lack of lakes with a February mean air temperature between ca 11 and 13 ºC (**Fig. 6.1**). Further sampling should target this gap. This is particularly important as this temperature range appears to represent a major chironomid ecotone. One of the requirements for optimal transfer-function performance is that the sample sites in the training set should be evenly spaced along the environmental gradient in question (Rühland and Smol, 2002).

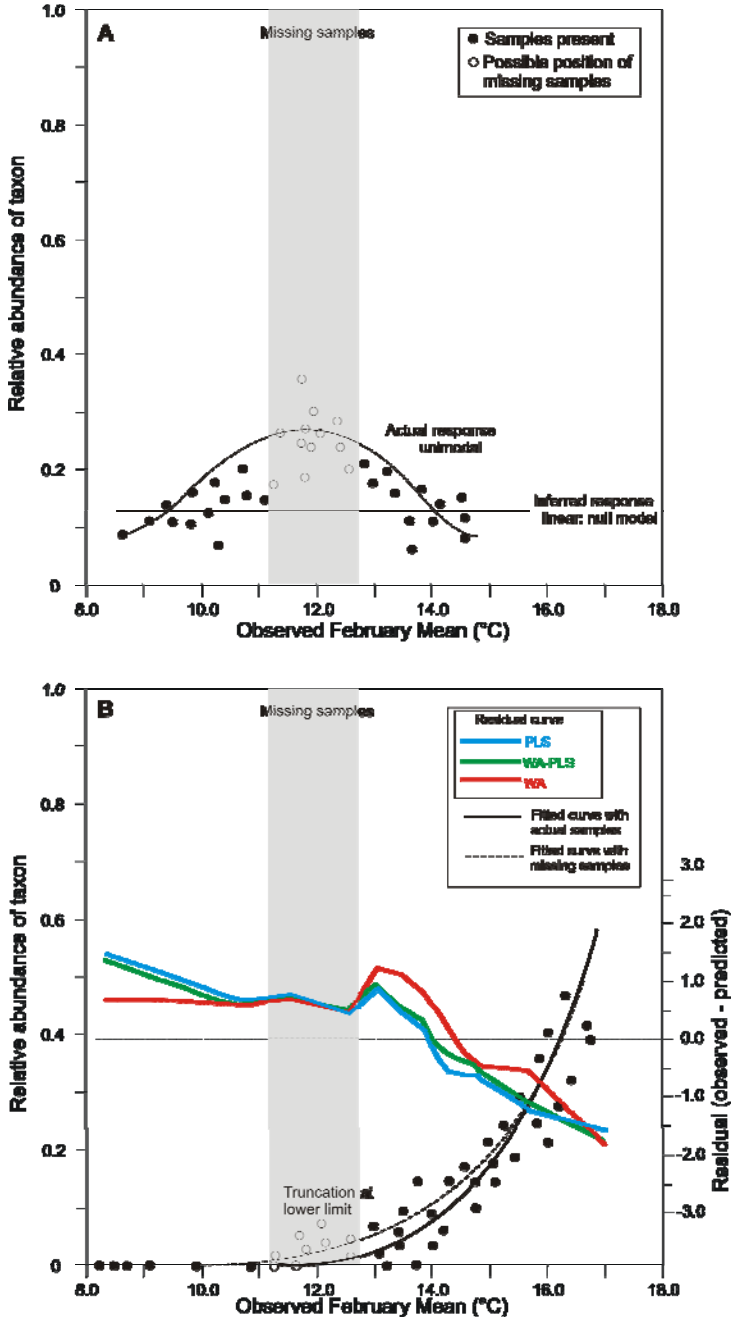


Fig. 6.8: Possible effects of the paucity of lake samples In the 11 – 13 ºC temperature range. **A.** If the taxon optimum is located somewhere in this temperature range, the best fitted GLM may be a null model, when the actual response is unimodal. This is an extreme case. A more likely scenario is the reduction of the significance of a unimodal response model. **B.** This temperature range coincides with the treeline. This appears to correspond to a major ecotone (maximum faunistic turnover). The temperature gap in this case could result in a truncation of the lower temperature threshold of taxa with a lower limit in this temperature range. This could result in an over prediction of temperatures close to this temperature range. Residual plots for unimodal and linear methods show that this is the case. It is usual for transfer-functions to over-predict and under-predict at the lower and upper limit of the gradient. However, there is a peak of over-estimation just below the sample gap. This is most pronounced for the weighted averaging (WA) model.

The paucity of samples with February mean air temperatures between 11 and 13 ºC may reduce the significance of fitted GLMs or result in a null or linear model, especially if the taxon optimum is located in this temperature range (**Fig. 6.8A**). This could be the case with *Corynocera* sp. The best fitted model for this taxon was a linear null model. A unimodal GLM with an optimum of 12.15ºC had a low (P= 0.106) significance (**Table 6.4**). The inclusion of more data-points between 11 and 13 ºC may improve the significance of the unimodal model. The sample gap may also cause a truncation of the lower temperature threshold in the temperature models (**Fig. 6.8B**). This could result in an over-prediction of temperatures just below this sampling gap. This seems to be the case with all of the temperature models. There is a peak in the residuals centred on 13 ºC (**Fig. 6.4, 6.8B**). Two common species (*Cladopelma curtivalva* and *Polypedilum* spp.) displayed a negative sigmoidal correlation to temperature (**Fig. 6.4**). *C. curtivalva* is an important temperature indicator species. *C. curtivalva* is not present above the sampling gap, and it is likely that the modelled response of this species represents an example of threshold truncation.

Total nitrogen:

The WA-PLS based inference model had the highest r^2 (0.8) and lowest RMSEP (0.179 Log_{10} TN/L) (**Table 6.3**). There also seemed to be less of a trend in the residuals with the WA-PLS model than the WA and PLS models. There was an obvious tendency for the WA model to over-predict the trophic status of lakes at the lower end of the TN gradient (**Fig. 6.4**). This model might therefore be unsuitable for determining the trophic status of a waterbody prior to the input of nutrients associated with intensive agriculture. The performance and residual trends were similar for the WA-PLS and PLS models. Even though the PLS model had a lower r^2 and higher RMSEP, it produced a lower mean and maximum bias (**Table 6.3**). It would therefore be appropriate to apply both models and compare the resulting reconstructions.

Only six out of the 17 taxa (35.2%) used in the final TN model had a significant response (P< 0.05) to the TN gradient (**Fig. 6.5, Table 6.5, 6.8**). This is similar to the proportion with a significant response to total phosphorus (TP) reported by Lotter et al. (1998) (34.5%) and Brooks et al. (2001) (44.1%). A non-significant response to TN could because these taxa are controlled by other environmental factors, or due to the size of the sample set. More data pertaining to some of the taxa that were scarce in this training set may serve to constrain their variation along the trophic gradient.

The removal of the non-significant taxa in this study reduced the performance of the WA-PLS model (Table 6.8). The removal of the non-significant taxa did improve the performance of the PLS

model. This resulted in a reduction of the RMSEP from 0.185 to 0.158 Log_{10} (TN) mg/L, which is a reduction of ~ 14.5%. The resulting model was based on 3 components, whereas the original model only required 2 components. The performance of this TN transfer-function is similar to the TN model produced by Brodersen and Anderson (2002) from a 41 lake training set from Greenland (**Table 6.8**). The r^2 for the model resulting from this thesis is much higher than the model produced by Brodersen and Anderson (2002). The RMSEP for the Brodersen and Anderson (2002) model is particularly low (0.07 Log_{10} (TN) mg/L). However, there was a strong correlation between temperature and trophic variables in the Greenland training set. There was also a high correlation between the WA temperature and trophic optima ($r^2 = 0.87$). Even though the apparent RMSEP is low, the confounding effect of temperature and TN in the Greenland training set makes the resulting transfer-functions unreliable.

Chironomid-based transfer-functions have also been created for other trophic variables. Brodersen and Lindegaard (1999) created a chironomid-based transfer function for chlorophyll *a* (Chla) based on a 54 lake training set from Denmark. Brodersen and Lindegaard (1999) have produced what appears to be a robust Chla model, but the exploratory data analyses are insufficient to ensure that the transfer-function is actually reconstructing Chla. A canonical correspondence analysis (CCA) of the taxonomic and environmental data revealed that Chla was significantly ($P < 0.001$) correlated to CCA axis 1 (canonical coefficient (cc) = -0.59). However, pH was also significantly correlated to CCA axis 1 (cc = -0.52). Brodersen and Lindegaard (1999) only included data for total phosphorus (TP), TN, Chla, pH, and Secchi depth in the CCA. The effect of temperature was not considered in the Denmark training set. The TP transfer function developed by Lotter et al. (1998) from a 48 lake training set from the Swiss Alps (**Table 6.8**) may suffer from a similar problem, especially since a temperature transfer function was also developed from the same training set. The effect of TP and summer water temperature may also be confounded in a 44 lake training set from the United Kingdom (Brooks et al., 2001). A transfer function was created for TP, while both TP and summer water temperature were significantly correlated to CCA axis 1.

Two other transfer-functions for lake trophic variables exist in New Zealand. Reid (2005) has created diatom-based transfer functions for isothermal mean Chla and annual mean TP (**Table 6.8**). It is interesting to note that a TP transfer function was created in this instance, even though only pH, Chla, electrical conductivity (EC) and nitrate/nitrite (NO_x-N) emerged as significant ($P < 0.05$) forward selected variables in the paper published by Reid (2005). Reid (2005) did not publish any results of partial CCAs. This is particularly important because the published CCA plot of the forward selected variables shows a high degree of colinearity between Chla and electrical

Dataset	# Lakes in model	Taxa removed	Taxa included	Model	Components	All jacknifed statistics				
						r^2	RMSEP (^oC)	RMSEP as % of gradient	Av. bias (^oC)	Max. bias (^oC)
All taxa all sites	43	0	51	WA-PLS	2	0.65	1.68	16.9	0.056	3.4
2% taxon deletion all sites	43	32	19	WA-PLS	2	0.62	1.77	17.8	-0.047	2.52
All taxa disturbed sites removed	31	4	47	WA-PLS	2	0.64	1.51	20.6	-0.018	1.99
2% taxon deletion, disturbed sites removed	31	34	17	WA-PLS	2	0.70	1.34	18.4	-0.089	1.77
Non-significant taxa and disturbed sites removed	31	42	9	WA-PLS	1	0.64	1.49	20.4	-0.320	2.51
Non-significant taxa and disturbed sites removed	31	42	9	WA		0.64	1.46	20	-0.050	2.72

Table 6.6: Comparison of the perormance of the best transfer-function based on various deletion criteria for species and sites. Removal of all taxa that were not present at at least a 2% abundance in at least 2 lakes resulted in the best performance with all lakes included and the disturbed sites removed. Removal of the taxa without a significant response to temperature (**Table 6.4, Fig. 6.4**) reduced the performance of the transfer function. Removal of the disturbed sites without the 2% taxon deletion resulted in an almost identical r^2, but improved the error (RMSEP).

Authors	Variable	Species data	Study area	#of lakes	#of taxa	% taxa sig. resp.	Model type	Comp.	r^2_{jack}	$RMSEP_{jack}$ (^oC)	RMSEP as % of gradient	Mean bias	Max bias
	Temperature (^oC)												
This study	**February mean air**	**Chironomids**	**New Zealand**	**31**	**17**	**52.9**	**WA -PLS**	**2**	**0.7**	**1.34**	**18.4**	**-0.089**	**1.773**
This study	**February mean air**	**Chironomids**	**New Zealand**	**31**	**17**	**52.9**	**WA**		**0.74**	**1.28**	**17.5**	**-0.204**	**1.965**
Larocque et al. (2001)	July mean air	Chironomids	Northern Sweden	100	42	69.8	WA -PLS	2	0.65	1.13	15.7	0.025	2.10
Brooks & Birks (2001)	July mean air	Chironomids	Norway and Svalbard	109	119	-	WA-PLS	3	0.94	0.90	7.4	-	0.59
Lotter et al. (1999)	July mean air	Chironomids	Swiss Alps & E. Canada	90	57	88.0	WA-PLS	2	0.81	1.74	10.9	-0.053	3.753

Table 6.7: Performance statistics for the the WA and WA-PLS chironomid-based temperature transfer functions compared to the model performance of three other temperature models from other parts of the world % taxa sig. resp. = the number of taxa with a significant response to the temperature gradient, Comp. = number of components.

Authors	Variable	Species data	Study area	#of lakes	#of taxa	% taxa sig. resp.	Model type	Comp.	r^2_{jack}	$RMSEP_{jack}$	RMSEP as % of gradient	Mean bias	Max bias
	Log_{10} (Chlorophyll *a*) (mg/L)												
Brodersen & Lindegaard (1999)	Summer mean chlorophyll *a*	Chironomids	Denmark	54	41	-	WA		0.67	0.65	32.99	0.005	0.92
Reid (2005)	Isothermal mean chlorophyll *a*	**Diatoms**	New Zealand	49	153	-	WA		0.71	0.18	14.2	0.001	0.265
	Log_{10}(TP) (mg/L)												
Brooks et al. (2001)	Annual mean TP	Chironomids	United Kingdom	44	72	44.1	WA		0.60	0.34	14.60	-0.006	0.84
Lotter et al. (1998)	Mean TP for circulation period	Chironomids	Swiss Alps	48	59	34.5	WA-PLS	2	0.68	0.139	13.76	-0.003	0.206
Reid (2005)	Annual mean TP	**Diatoms**	New Zealand	48	153	-	WA		0.50	0.24	19.52	-0.004	0.221
	Log_{10}(TN) (mg/L)												
Brodersen and Anderson (2002)	Mean TN concentration	Chironomids	Greenland	41	17	-	WA		0.56	0.07	4.5	-0.002	0.21
This study	**Summer TN concentration**	**Chironomids**	**New Zealand**	**30**	**17**	**35.2**	**WA-PLS**	**2**	**0.80**	**0.179**	**11.4**	**0.0008**	**0.326**
This study	**Summer TN concentration**	**Chironomids**	**New Zealand**	**30**	**6**	**100**	**PLS**	**3**	**0.84**	**0.158**	**10.1**	**-0.002**	**0.367**
This study	**Summer TN concentration**	**Chironomids**	**New Zealand**	**30**	**6**	**100**	**WA-PLS**	**2**	**0.79**	**0.179**	**11.4**	**0.012**	**0.361**

Table 6.8: Performance statistics for the chironomid-based TN model from this study compared with other chironomid-based lake trophic status proxy models (Brooks et al., 2001; Lotter et al., 1998), a chlorophyll *a* model (Brodersen & Lindegaard, 1999), and a New Zealand diatom-based TP model (Reid, 2005). % taxa sig. resp. = the number of taxa with a significant response to the temperature gradient. Comp. = number of components. Note that the removal of all insignificant taxa (**Table 6.5**, **Fig. 6.5**) makes only a slight improvement to the r^2 and RMSEP but inceases the mean and maximum bias for the WA-PLS and PLS models.

conductivity (EC). This is a concern, especially since Cochran (2002b) has produced a New Zealand diatom-based transfer function for EC. Surprisingly, the TN transfer-functions produced from this study are quite robust, even though the TN concentration data was based on "spot" samples taken once during the summer of a single year. Obviously for the sake of transfer-function development it is important that the species data from the modern training set represents the same period of time as the environmental data, or that the environmental data is representative of the period of time when the sub-fossil remains were deposited. The majority of the chironomid assemblages (22 out of 32) in the lowland training set were taken from the top 1 cm of the surface sediment sample. It was necessary to sample deeper horizons (2-3cm) for 9 of the lakes in the lowland training set.

It is likely that these surface sediment sample intervals represent different periods of time in different lakes, depending on the sedimentation rate. There are a limited number of studies that provide age/depth data for lake sediments from the sediment/water interface in New Zealand. Gall and Downes (1997) provide ^{210}Pb age vs depth curves for the sediment/water interface from four North Island lakes. The four lakes sampled (Okareka, Okaro, Okataina, and Rotorua) ranged in size from 0.28 to 79.8 km^2 and their mean depths ranged from 10 to 44 m. Lakes Rotorua and Okaro are situated in heavily modified catchments (agriculture, urbanisation etc.) while the catchments of Okareka and Okataina are largely unmodified. The top 1cm represented a period of deposition ranging between 1 and 8 years for these four lakes. The top 1 cm represented a shorter period of time in the lakes situated in heavily modified catchments (e.g. Rotorua) and a longer period of time in the lakes situated in largely undisturbed catchments (e.g. Okataina).

I would therefore expect the surface sediment samples in the lowland training set to represent at least 2 years deposition. There are three main sources of variation at this time scale that could provide a discrepancy between time period represented by the measured trophic status (TN) and the modern chironomid assemblage. These three sources are intra-seasonal, inter-seasonal and inter-annual environmental variation.

The most extreme inter-seasonal variation would be expected to occur in shallow, eutrophic lakes. An example is provided in **Fig. 6.9** of the typical variation in water temperature, TN concentration and the frequency of hypolimnetic anoxia in a shallow, warm monomictic or discontinuous polymictic lake. TN concentrations for this study were measured using the alkaline persulfate digestion method, and are therefore representative of the concentrations of organic nitrogen, ammonium, nitrate, and nitrite. Elevated TN concentrations during the summer can be caused by a variety of mechanisms, including fixation of atmospheric nitrogen by cyanobacteria. Increased evaporation and reduced effective precipitation during summer may lead to increased

solute concentrations and reduced lake levels. Reduced lake levels may increase wind driven sediment re-suspension, resulting in the release of organic bound nitrogen into the system.

Studies of the annual larval life cycles and production of the New Zealand Chironomidae are limited (Forsyth and Callum, 1983; Graham and Burns, 1983). It would be safe to assume that at least some of the New Zealand taxa are multivoltine, i.e. they pass through several generations each year.

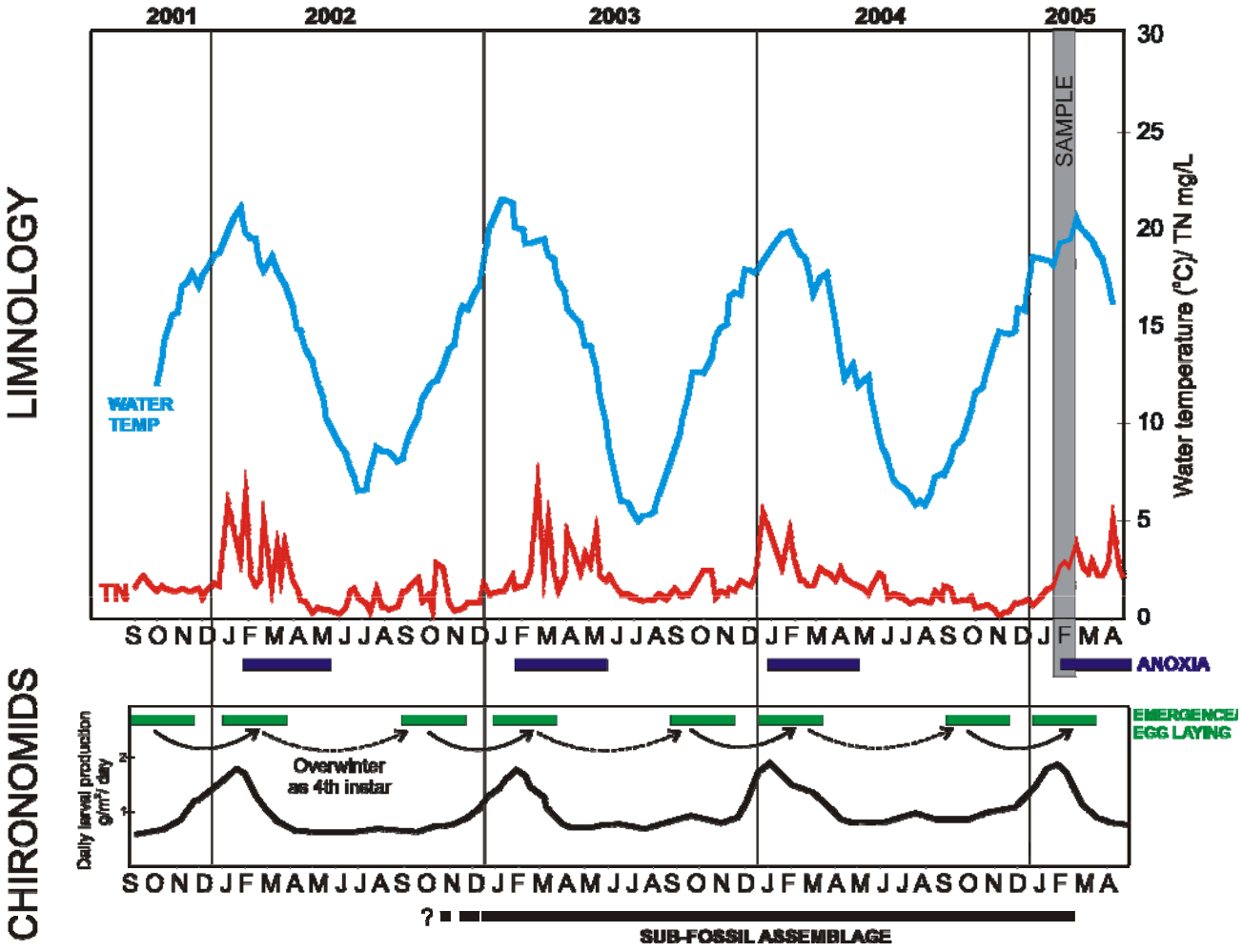


Fig. 6.9: Comparison of the annual and inter-annual variation in the limnology of a shallow, lowland, eutrophic (Lake Forsyth) (Canterbury Regional Council, unpublished data) and the life cycle and larval production rate of a typical New Zealand chironomid: *Chironomus* spp. from Lake Hayes (Graham and Burns, 1983). This life cycle pattern is also typical of *Polypedilum* spp. (Forsyth and McCallum, 1983) The surface sediment samples in the training set are likely to represent at least 2 years of deposition. In the case of *Chironomus* spp., this represents at least 4-5 generations. Conversely, the surface water sample is instantaneous, and represents 1 day in summer of a particular year. At least in the case of *Chironomus* spp. initiation of each life cycle occurs in the spring or summer, when TN concentrations are elevated, but not necessarily maximum. Survival of the summer generation is dependent on the ability to survive anoxia, and reduced winter temperatures.

In the worst case scenario (as far as spot summer measurements are concerned) the chironomid taxa may complete life cycles during the summer and winter. This may be the case for the lotic taxa (e.g. *Cricotopus* spp.) as multivoltinism is generally more common in lotic taxa in other parts of the world (Tokeshi, 1995). Voltinism may be another factor affecting the significance of the relationship between taxon abundance and TN concentration in this training set. If the taxa included a large proportion of multivoltine taxa, it would be more appropriate to use an annual mean TN concentration.

Several studies have been performed for two of the taxa that did display a significant relationship to summer TN concentration, i.e. *Chironomus* spp. and *Polypedilum* spp. (Forsyth and Callum, 1983; Graham and Burns, 1983). A summary of the life cycle and daily larval production rate, based on data from these publications is provided in **Fig. 6.9**. Both taxa complete one life cycle between the start of spring (September) and late summer (February). A second life cycle is initiated in late summer (February) and is not completed until the spring. Therefore at least part of the spring generation could possibly experience elevated TN concentrations and lake production, but only the late summer generation would experience elevated TN concentrations, lake production and anoxia. The late summer generation may also over winter as late 4^{th} instar larvae, so it would also be necessary to be able to endure low winter water temperatures.

The timing of the water sampling corresponds with a peak in the observed chironomid larval production rate observed in *Chironomus* spp. (Graham and Burns, 1983) (**Fig. 6.9**). If this is the case with many of the other common New Zealand chironomid taxa, this could explain why a February TN concentration has resulted in such a robust transfer-function. Even though chironomid taxa may initiate or complete life cycles at other times during the year, this period is a critical period for larval production. This period is also critical as it would coincide with the beginning of emergence and egg laying by the summer larval generation, which is critical determinant for the spring population of the following season.

A more comprehensive water sampling regime would provide data that is more representative of the time period represented by the surface sediment assemblages (e.g. mean annual TN concentrations). This may result in a more significant relationship between taxon abundance and TN concentration, and more reliable transfer-functions. The current trophic classification system for New Zealand lakes (Burns et al., 2000) is based on mean annual TN concentrations. Using mean annual TN concentrations for transfer-function development would mean that trophic level reconstructions are more meaningful in the context of this classification system.

6.3 Conclusions:

The transfer-functions produced by this study for mean February air temperature and total nitrogen (TN) compare favourably to chironomid-based temperature and trophic transfer-functions produced from other parts of the world. The February mean transfer-functions were not as robust as the TN transfer-functions, despite the fact that mean February temperature data was used. The performance of the temperature transfer functions could be improved by increased taxonomic resolution (particularly for *Chironomus* spp.), increasing the gradient length, and a more even distribution of samples along the temperature gradient. A paucity of samples in the training set between 11 and 13 ^{o}C is one possible source of error. This sample gap may result in an over estimation of temperatures below this temperature range, and a reduction in the significance of the taxon response models to this environmental variable.

The TN transfer-functions were particularly robust, and outperformed the existing diatom-based transfer-functions for reconstructing the past trophic status of New Zealand lakes. The excellent performance of the TN models is surprising, considering that the TN concentrations were based on single water samples taken during the summer of a single year. The limited data that is available on New Zealand chironomid larval production ecology suggests that February is critical time for larval production in New Zealand lowland lakes. This period coincides with the initiation of emergence and egg laying by the summer generation. A more comprehensive water sampling regime, at least for the entire spring-summer period may result in more representative environmental data. Annual mean TN concentrations would be more appropriate where the proportion of multivoltine taxa is high. The reconstruction of annual mean TN concentrations would also result in values that make more sense in the context of the current trophic definitions for New Zealand lakes, which are based on annual mean nutrient concentrations.

CHAPTER 7: APPLICATION OF THE CHIRONOMID-BASED TRANSFER FUNCTIONS.

PART I: RECONSTRUCTION OF SUMMER AIR TEMPERATURE FROM LAKE DEPOSITS IN LYNDON STREAM, NEW ZEALAND, SPANNING THE MIS 3/2 TRANSITION

7.1 INTRODUCTION

7.1.1 General introduction

This chapter presents the results from the first application of the chironomid-based temperature transfer-function developed in the previous chapter. The content of this chapter is largely based on a paper that is currently in press with Quaternary Science Reviews (Woodward and Shulmeister, inpress, **Appendix D**). The transfer-function that was used to create the temperature reconstructions and ordination plots in the published paper utilised a slightly different dataset to the temperature transfer function presented in **Chapter 6**. The temperature transfer-function used in the Quaternary Science Reviews paper was based on a dataset (n = 35) with the five most productive lakes (chlorophyll $a \geq 9$ μg/L) removed. A further four lakes productive lakes (Lake Okaro, Hayes, Tutira, and "Mill") were removed during the development of the temperature transfer function used for the temperature reconstructions in this thesis (**Chapter 4**,**5**, and **6**). The reasons for removing all of the lakes situated in catchments with a significant amount of human disturbance are given in **Chapter 4, Section 4.4.3**.

7.1.2 Background

The ability to accurately reconstruct past climates is a reflection of our capability to predict major climate change in the future. Since the initiation of CLIMAP (Climate Long-range Investigation, Mapping, And Prediction) almost thirty years ago (CLIMAP project members, 1976) the Last Glacial Maximum (LGM) (23,000 to 19,000 cal yr BP (Mix et al., 2000) has remained an important benchmark for the testing of global climate models. The LGM represents the most recent, well-recorded, example of major natural climate change that lies within the limits of a large number of

dating techniques. Therefore it is possible to obtain a large amount of paleoclimatological data which not only serves to validate climate models but direct their construction.

Recent studies (Crowley and Baum, 1997; Crowley, 2000; Kohfeld and Harrison, 2000; Moreno et al., 2005) have emphasised the importance of an 'earth-system' approach to model development; climate models should account for possible effects of ocean-atmosphere-cryosphere-biosphere interactions. Global climate models have, until recently been based largely on reconstructions of sea surface temperatures (SSTs) (e.g. CLIMAP 1981) because SST reconstructions are based on a globally extensive dataset of modern analogs (e.g. Barrows and Juggins, 2005). However, observations based on an ever increasing terrestrial dataset (e.g. dust records, lake-levels, faunal and floral based reconstructions, and paleo snow-line elevations) have revealed inconsistencies between terrestrial conditions inferred from SST-based global climate models and inferences based on local proxy data (Pinot et al., 1999).

Terrestrial paleoclimate data from the Northern Hemisphere far exceeds the quantity of data from the southern latitudes. The few quantitative estimates for land-based LGM temperature anomalies in the Southern Hemisphere have been based on snow-line depressions (Hilton et al., 1994; Bacon et al., 2001), TEX_{86} lake surface temperatures (LSL) (Powers et al. 2005), and pollen-based estimates (e.g. Bush et al., 2004). Increasing this dataset is essential for the purposes of global climate model development and validation.

Despite being identified as a key site for future investigation into LGM climate variability (Broecker, 1997), quantitative paleoclimate data generated for the LGM period in New Zealand are also limited. These data are especially important, as recent studies (Suggate and Almond, 2005; Vandergoes et al., 2005) indicate that so called 'LGM' cooling in New Zealand may have begun as early as 34,000 cal yr BP; predating the real LGM by 11,000 years. The last glacial cycle (ca 74,000 to ca 11,500 cal yrs BP) is locally known as the Otira Glaciation (Suggate, 1990). In this thesis I refer to the period between 34,000 and 18,000 cal yrs BP in New Zealand which corresponds to a series of major ice advances (Suggate and Almond, 2005) as the late Otiran glacial sequence (LOGS).

I avoid the use of the term LGM as the term 'LGM' as it is officially defined denotes the last period of maximum global ice volume (Mix et al., 2000). The use of this term to label local ice advances (even though there are Southern Hemisphere correlatives (Denton et al., 1999b)) has already caused confusion. I use the term 'sequence' because there were several major ice volume fluctuations in New Zealand during this time (Suggate and Almond, 2005) and a great deal of climate variability (Sandiford et al., 2001, 2003; Hägg and Augustinus, 2003; Hormes et al., 2003;

Vandergoes et al. 2005). Although some large ice advances occurred early in the LOGS (Suggate and Almond, 2005) it appears that the greatest amount of cooling did not occur until the time of the global LGM (Barrows and Juggins, 2005).

Pollen-based estimates imply mean annual temperature (MAT) depressions for the LOGS ranging from 4 - 7 ^{o}C (Soons, 1979; Shulmeister et al., 2001). Beetle-based MCR (mutual climate range) reconstructions from the middle (ca 27,000 to 22,000 cal yrs BP) of the LOGS suggest a maximum cooling of between 1.9 and 5 ^{o}C in summer (February mean) and 2.2 and 6 ^{o}C for winter (July mean daily minimum) (Marra et al., 2004; Marra et al., 2006).

Previous studies elsewhere in the world (Seppa et al., 2004) have used pollen-based transfer functions to infer past climate conditions. Despite the fact that pollen has been the most widely used proxy for climate change in New Zealand, only one study (Norton et al. 1986) has explored the possibility for the development of pollen-based transfer functions. The resulting transfer functions were not robust enough to be confidently applied to the fossil pollen record. Therefore generalisations about climate have continued to be inferred from the modern species distribution of taxa found in the fossil record. A major climate deterioration spanning the entire LOGS has been inferred from the low abundance of pollen belonging to canopy trees (Podocarpaceae and *Nothofagus*) and the abundance of herb and grass pollen in records spanning approximately 34,000 to 18,000 years ago (Moar, 1980; Moar and Suggate, 1996; Vandergoes et al., 2005 (**Fig. 7.10**)).

Very little cooling has been inferred from some of the beetle-based reconstructions (Marra et al., 2004; 2006) and from recent climate model-based air temperature inferences (Weaver et al., 1998; Bush and Philander, 1999). A slight increase in canopy tree pollen abundance is recorded in some LOGS pollen records at the MIS 3/2 transition (Vandergoes et al., 2005). However, if the inferences of mild cooling from other proxies are correct, most of the North Island and the northern half of the South Island below 600-700m above sea level (asl) should have been forested (McGlone, 1993). Therefore a number of other environmental factors including altered CO_2 regimes, fire, drought, invasion of cold maritime polar air masses, and strong winds have been cited as possible causes for the lack of forest cover during the New Zealand LGM (McGlone and Bathgate, 1983; McGlone, 1985, 1988).

This chapter presents results of the first chironomid-based summer temperature reconstructions from lake deposits in New Zealand. The site reported comes from the banks of Lyndon Stream in the high country of Canterbury, on the eastern side of South Island of New Zealand (**Fig. 7.1**) and lies in the middle (~26,500 to 24,500 cal yr BP) of the LOGS. Studies elsewhere in the world have validated the ability for chironomid-based transfer functions to predict air temperatures (Walker et

al., 1991; Olander et al., 1997). The locality was chosen because there are existing qualitative temperature estimates based on macrofossils (Soons and Burrows, 1978) and quantitative temperature estimates from beetles (Marra et al., 2006) for this site. This study resulted in temperature estimates for the complete section of lake silts preserved at this site. The results from this study serve not only to provide a more complete picture of climate conditions in New Zealand during the LOGS at this locality, but also enable comparison of the chironomid-based temperature estimates with independent proxies.

7.2 SITE DESCRIPTION

7.2.1. Physiography and site context

Lyndon Stream is located in the Acheron Valley, in the eastern foothills of the Southern Alps, South Island, New Zealand (**Fig. 7.1**). The study site is at an altitude of 700m asl. Locally, the eastern foothills reach elevations of up to 2300 m and are composed largely of moderately indurated Triassic-Jurassic metasediments belonging to the Torlesse Supergroup (Bradshaw, 1972). The local geomorphology has been profoundly influenced by a series of Late Pleistocene glacial advances (Soons, 1963; Suggate, 1990). Of particular relevance to this study, are the multiple ice advances from west to east along the upper reaches of the Rakaia River (**Fig. 7.1**) (Soons, 1963). Moraines and outwash terraces in the Rakaia valley provide evidence for five main glacial sequences, locally named the Acheron, Bayfield (inferred to be late Otiran in age), Tui Creek, Woodlands and Hororata advances (in order of increasing age) (Soons and Gullentops, 1973).

The Acheron Valley is a splay valley of the Rakaia and the valley is partly occupied by moraines and outwash fans of the Rakaia Valley glaciers. A series of three moraine ridges lies at the southern end of the Acheron Valley (Fig. 1). Soons and Burrows (1978) argued that these moraines represented glacial limits during the Bayfield ice advance in the Rakaia Valley. Two early advances (Bayfield 1 and 2) are represented by the two highest moraine ridges, while the Bayfield 3 advance is represented by the lowest of the three moraines (**Fig. 7.1**). The Lyndon Stream sediments have been deposited in an incision in the Bayfield 2 outwash surface (**Fig. 7.2**). Therefore the deposition of the Lyndon stream sediments post-dates Bayfield advances 1 and 2 and pre-dates the Bayfield 3 advance. Radiocarbon ages from the deposit (Soons and Burrows, 1978) confirm a middle LOGS age for these deposits and are in fact the only published age control on the Bayfield advances in the Rakaia system.

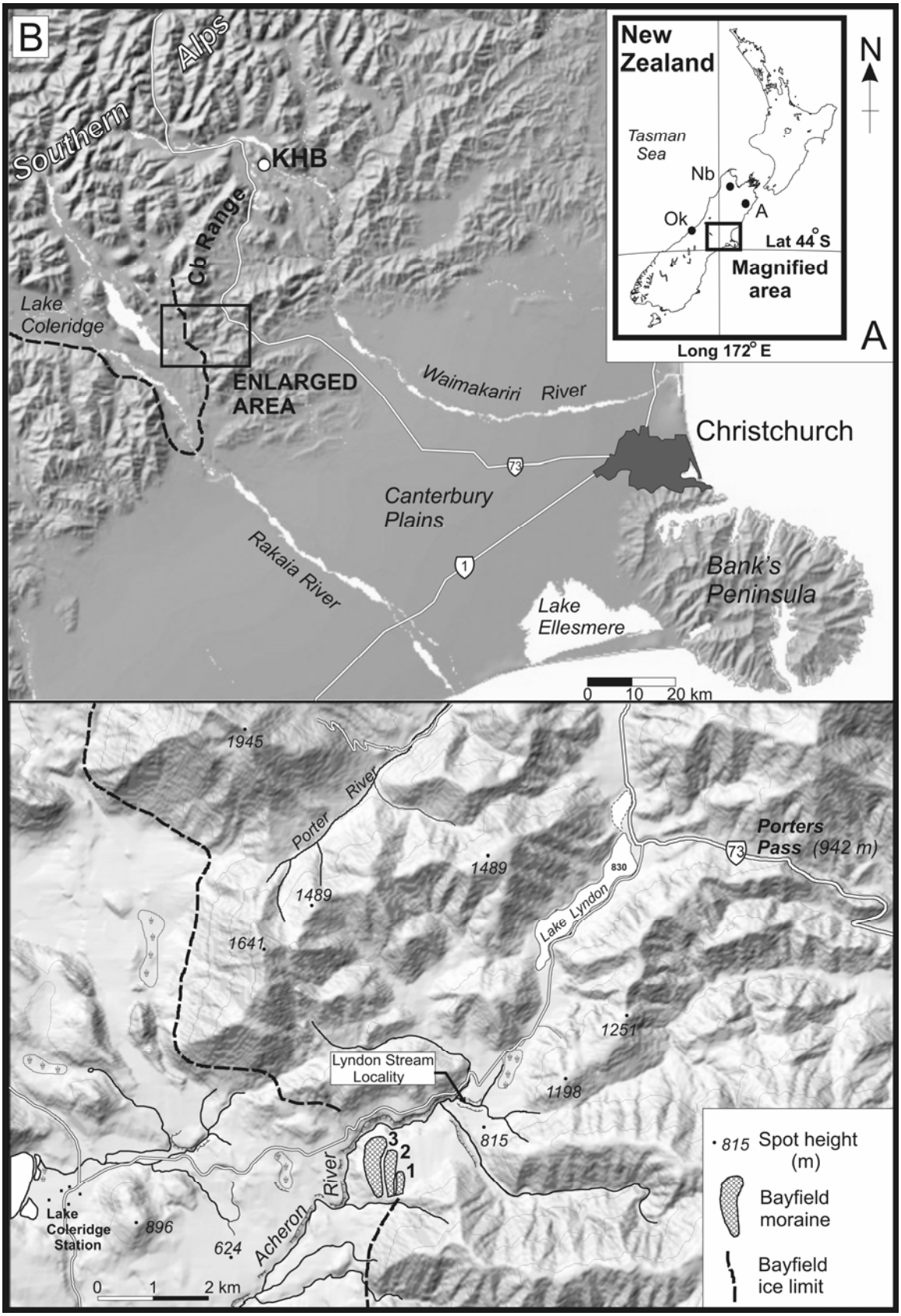


Fig. 7.1: The location of the study site and other features mentioned in the text. A) Ok = Okaritio Bog, Nb = Nettlebed Cave, A = Awatere Valley. B) Cb Range = Cragieburn Range, KHB = Kettlehole Bog.

7.2.2. Climate

The local climate is a product of the interaction of the Southern Hemisphere westerlies with the rugged topography of the Southern Alps (Sturman and Wanner, 2001). Orographic uplift of the airflow off the Tasman Sea results in an extreme contrast in average rainfall between the western and eastern sides of the mountains. Average annual precipitation near the divide on the western side of the Southern Alps can reach well over 10,000 mm, while the eastern coastal plains and mountain basins receive an average annual rainfall of 600 mm (Griffiths and McSaveney, 1983).

The mean annual total rainfall at the Lake Coleridge climate station (364 m AMSL) about 8 km west of the site (**Fig. 7.1**) is 833 mm (NIWA, unpublished data). The mean annual temperature at the same station is 10.4 ^{o}C. The late summer (February) mean (14 ^{o}C) and winter (July) mean minimum (-1 ^{o}C) for the study site was extracted from a climate surface fitted to data from 346 weather stations covering a period of 30 years (Leathwick et al., 1998). Salmon (1992) reported temperature data for the tree-line (1341 m asl) from the nearby Cragieburn Range (**Fig. 7.1**). The February mean for this altitude was 10 ^{o}C, while the July mean minimum was -3.5 ^{o}C.

7.2.3 Vegetation

Pollen records (Burrows and Russell, 1990) and macrofossils (Burrows, 1995) provide evidence for the existence of a mixed podocarp/angiosperm (e.g. *Prumnopitys taxifolia*) forest in the lowlands and a *Nothofagus* (*N. solandri* var *cliffortoides*) forest on the higher slopes (up to 1400m) from at least 3000 years ago. Only patches of this original forest cover remain, after being largely destroyed by fire in the last 800 years after the arrival of Polynesians (ca 1300 AD) and Europeans (ca 1840) (Burrows and Russell, 1990; McGlone & Wilmshurst, 1999). Short-tussock grassland (*Festuca novae-zelandiae* and *Poa colensoi*) and patches of scrub (*Leptospermum scoparium*, *Discaria toumatou*, *Ozothamnus leptophyllus*, *Coprosma propinqua*, *Hebe* spp., and *Dracophyllum* spp.) form the dominant vegetation cover at present.

7.2.4 Stratigraphy and lithology

The Lyndon Stream has incised a ~14m deep gully into the sediments on the eastern side of the Acheron Valley, exposing a sequence of glacial outwash, lake silts, sand, silt, and alluvium (**Fig. 7.2**). Soons and Burrows (1978) described the sedimentology for the entire section, and derived radiocarbon dates from organic material in the basal lake silts and upper *Sphagnum* silts. Macrofossils and pollen were also extracted from a sample from the base of the lake silts and described. The following description is a summary of Soons and Burrows (1978).

Basal 2 m:

Brownish grey till; upper 20-30 cm iron-stained

Discontinuity

≤6 m:

Fine blue-grey laminated silts, with plant remains consisting chiefly of *Myriophyllum elatinoides*. A conventional radiocarbon age of 22200 +/- 750 ^{14}C yr BP (NZ 3940) was obtained from a sample collected at the base of the silts where they overly the till.

2 m:

Brown laminated silts with occasional fine gravel layers.

2.5m:

Brown sands and silts with occasional fine gravel bands. *Sphagnum* silts occur at the top of this deposit. A conventional radiocarbon age was derived from the *Sphagnum* silts was 19,200 ^{14}C $\pm$ 550 yr B.P (NZ 4298).

Top 1.5m:

Locally derived subangular brown greywacke, horizontally bedded and alternating with brown sandy layers.

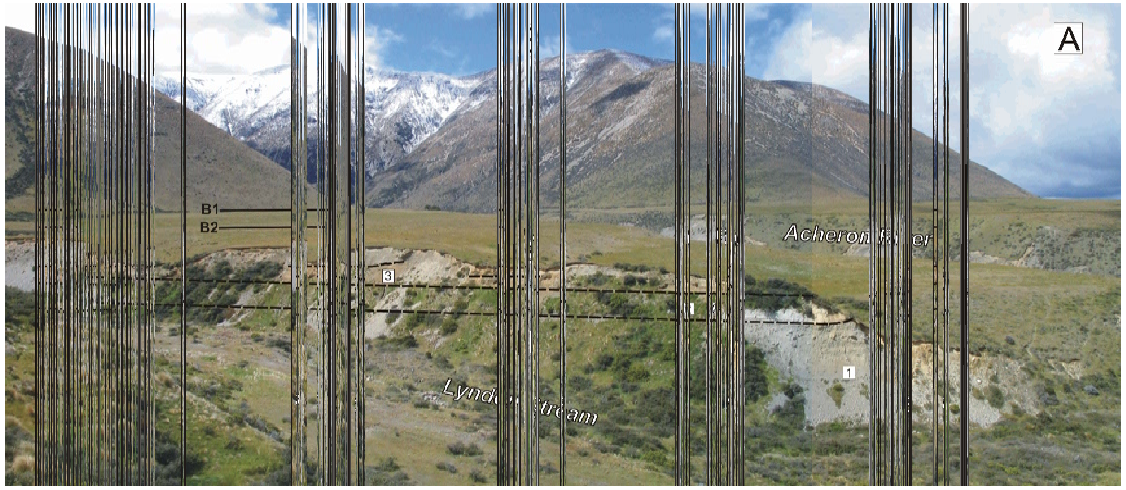


Fig. 7.2: **A. View south-west from the north-western side of Lyndon Stream. 1. Glacial outwash from the Bayfield 2 advance. 2. Bedded Lake silts deposited in an incision in the B2 outwash 3. Overlying Brown sands, silts with gravel packages. Bayfield 2 (B2) and Bayfield 1 (B1) outwash surfaces are in the background. B. Close up of the Lake silts (2) resting unconformably upon Bayfield 2 glacial outwash (1) . The upper contact is obscured by vegetation. C. Upper transition between the bedded lake silts (blue-grey) and the overlying brown sands, silts and gravels. Note the presence of ripples with mud drapes in the upper part of the section. Spade for scale (ca. 1m)**

7.2.5 Detailed description of the lake silts

This chapter deals with the chironomid stratigraphy of the lake silts, therefore a more detailed description of this horizon is provided in the following section.

The lake silts were carefully examined while samples were collected for this study. Soons and Burrows (1978) described a 6 m thick laminated lake silt horizon. I could not find an exposure in the Lyndon Stream cutting were the basal lake silts were 6m thick. The section sampled for this study was only ~ 3.5m thick (**Fig. 7.2A & B**). A close inspection of the lake silts also revealed that individual layers that were < 1cm thick were quite rare. Therefore it would be more accurate to describe the lake sediments as bedded (Schnurrenberger et al., 2003). True laminations were more common near the transition between the bedded lake silts and the overlying silts (**Fig. 7.2C**).

Individual beds ranged in thickness from 1- 10 cm and comprised alternating bands of light and dark coloured material. Bedding was particularly weak in places where bedding contacts were indistinct (change noted over > 1 cm) and individual beds were discontinuous. Undulating contacts between beds were also common.

7.3 METHODS

7.3.1. Sediment sampling and processing

The entire section, from the base of the bedded lake silts to the top of the upper sandy-silt unit, was sampled at approximately 25 cm intervals for chironomid analysis. 2 cm thick slabs of sediment (~ 30 cubic centimetres) were removed from the outcrop face using a large sharp knife. Large sections of the upper sandy-silt unit appeared to be unsuitable for the preservation of chironomid remains (coarse grain size, evidence of low organic content, cross-bedding etc (**Fig. 7.2C**)). Therefore, samples were only taken from the fine grained silty-clay units that were present in this part of the section. A preliminary examination revealed that chironomids were absent even from these horizons in the upper sandy-silt unit.

Sediment samples were processed for chironomids following a modified version of the method outlined in Walker (2001). Samples were weighed, deflocculated in hot 10% KOH and washed through a 93 μm mesh with copious amounts of distilled water. Samples were then transferred to a Bogorov counting tray and examined for invertebrate remains under a dissection microscope at 50x

magnification. Heiri and Lotter (2001) and Quinlan and Smol (2001) have shown that a sample size of 45-50 head capsules provides an adequate representation of chironomid diversity in a sample. Sufficient sediment (typically 10 ml) was processed in order to obtain this minimum head capsule abundance.

Chironomid head-capsules were mounted on glass slides in a drop of lactophenol PVA and covered with a glass coverslip. Head-capsules were mounted ventral side up to facilitate identification. Chironomids were identified using a transmission light microscope with the aid of publications by Schakau (1993), Boubee (1983), Forsyth (1971), Winterbourne et al. (2000), and identification guides by Boothroyd (1994, 2002, 2004). The division of the genus *Chironomus* was based on unpublished morphological and karyotypic data from Jon Martin and Don Forsyth (see **Chapter 2, Section 2.3**).

A small sample from each horizon was weighed then dried in an oven at 100 ºC for 24 hours to allow the calculation of head capsule concentrations per gram of dry sediment. Oven dried samples were then heated to 550 ºC for 12 hours to allow the calculation of the organic content (loss-on-ignition) for each sample.

7.3.2 Data analysis and presentation of results

The abundance of each chironomid taxon was expressed as a percentage of the total head-capsule count for each individual horizon. Simuliidae ("black flies", *Austrosimulium*) head-capsules were also found, these were expressed as a percentage of the total head-capsule count (chironomids and Simuliidae combined). Taxon abundances were displayed relative to stratigraphic depth using the computer program C2 (Juggins, 2003). Zonation of the chironomid stratigraphy was achieved using the CONISS (constrained incremental sum of squares) function in Zone 1.2 (Juggins, 1992). The analysis was based on the chironomid percentage data standardized to a mean of zero and to unit standard deviation (Grimm, 1987). The Shannon Weaver Index (H') was used as a measure of chironomid diversity, $H' = -\Sigma\ Pi \ln Pi$, where Pi represents the proportion of the i^{th} taxon in the sample (Begon et al., 1986).

Exploratory analysis of the fossil chironomid assemblages from the Lyndon Stream site were investigated using CANOCO version 4.5 (ter Braak and Šmilauer, 2002). Fossil samples were plotted as passive samples in a canonical correspondence analysis (CCA) ordination plot of modern chironomid samples and environmental variables from the 31- lake temperature training set (**Chapter 4, 5 and 6**). Fossil samples were joined as a 'time-track' to allow the interpretation of

changes in fossil chironomid assemblage composition with respect to environmental parameters with a significant ($p \leq 0.05$) influence on the distribution and abundance of chironomid taxa in the temperature training set. Mean February air temperatures were reconstructed using the best selected WA-PLS, PLS, and WA transfer-functions (see **Chapter 6**) using the computer program C2 (Juggins, 2003). Bootstrapping cross-validation was applied to each model to allow the construction of sample specific errors. Temperature reconstructions were compared with a plot of the sample scores for the fossil samples with respect to CCA axis 1 which is predominantly a temperature gradient.

7.4. RESULTS

7.4.1. Chironomid stratigraphy

The results from the chironomid analysis are shown in a percentage diagram in **Fig. 7.3**. 15 chironomid taxa were recovered from the Lyndon Stream section. The most common taxon in the Lyndon Stream section belonged to the genus *Chironomus*. The other 13 taxa were present in low abundances (<10 %) for the entire section except for *Corynocera* and *Naonella forsythi*, which exceeded 10 % relative abundance in Zone 2 and Zone 4 respectively.

Until recently it was impossible to distinguish the three previously described *Chironomus* species from the New Zealand mainland (Hudson, 1892; Kieffer, 1922a; Freeman, 1959) based on head-capsule morphology alone. Jon Martin and Don Forsyth (unpublished) have performed extensive morphological and karyotypic studies of New Zealand *Chironomus* larvae and now conclude that nine species of *Chironomus* exist on the New Zealand mainland. However, it is only possible to reliably distinguish one of those nine species from the other eight based on head-capsule morphology alone.

Jon Martin and Don Forsyth (unpublished) identified *Chironomus* sp. a based on the larval karyotype and observed that this species always had a large number (> 60) striations on the ventromental plate. It is almost certain that this species is actually the *Chironomus zealandicus* that was originally described by Hudson (1892) (Jon Martin, pers. Comm.). Until this link is confirmed beyond doubt I will refer to this species as *Chironomus* sp. a. The other eight species identified by Jon Martin and Don Forsyth always had a smaller (< 60) number of striations on the ventromental

plate. All the head-capsules belonging to *Chironomus* from this record had less than 60 striations on the ventromental plate. I refer to this morphological type as *Chironomus* spp..

All of the *Chironomus* head-capsules in the temperature training set used in this study also belonged to the *Chironomus* spp. type (**Chapter 5**). *Chironomus* sp. a was only present in abundances ≥ 2% in the five highly productive (chlorophyll *a* ≥ 9 μg/L) lakes that were removed from the temperature training set. *Chironomus* sp. a was present in abundances ≤ 2% in two other lakes; a lowland mesotrophic lake and a high altitiude microtrophic lake (trophic definitions after Burns et al., 2000). Therefore the division of the *Chironomus* genus into two morphological types did not affect the performance of the temperature transfer-function.

The chironomid record was divided into four zones based on the total dispersion values produced by the CONISS cluster analysis in Zone 1.2. 2 species (*Chironomus* spp. and *Naonella kimihia*) dominated the chironomid assemblages for the entire section. The main distinctions between the four chironomid zones are the presence of Macropelopini and *Corynocera* in Zone 2, the gradual decline in abundance of *Naonella kimihia* from Zone 1 to Zone 4 and the appearance of a number of orthoclad taxa in Zone 4.

The average diversity for the entire record was low (H'= 0.4), with two peaks of slightly higher diversity in Zone 2 and Zone 4. Head-capsule concentrations were highest in Zone 1 (~ 50 - 80 head capsules g dry sediment $^{-1}$ (HC/g^{-1})) and dropped abruptly to remain low (< 10 HC/g^{-1}) for the rest of the record. Higher head-capsule concentrations also coincided with the tendency for a slightly higher organic content (≥ 5 % LOI) in the basal metre of the record.

Black fly (Simuliidae) head-capsules (*Austrosimulium*) were also present in low percentages in Zone 3 and 4. *Austrosimulium* counts were not included in the zone analysis. Percentage abundance of *Austrosimulium* was calculated as a fraction of all head-capsules (chironomids *and* Simuliidae). *Daphnia* (Cladocera) ephippia (resting eggs) were also common between 200 and 220 cm (the Zone 1/2 transition).

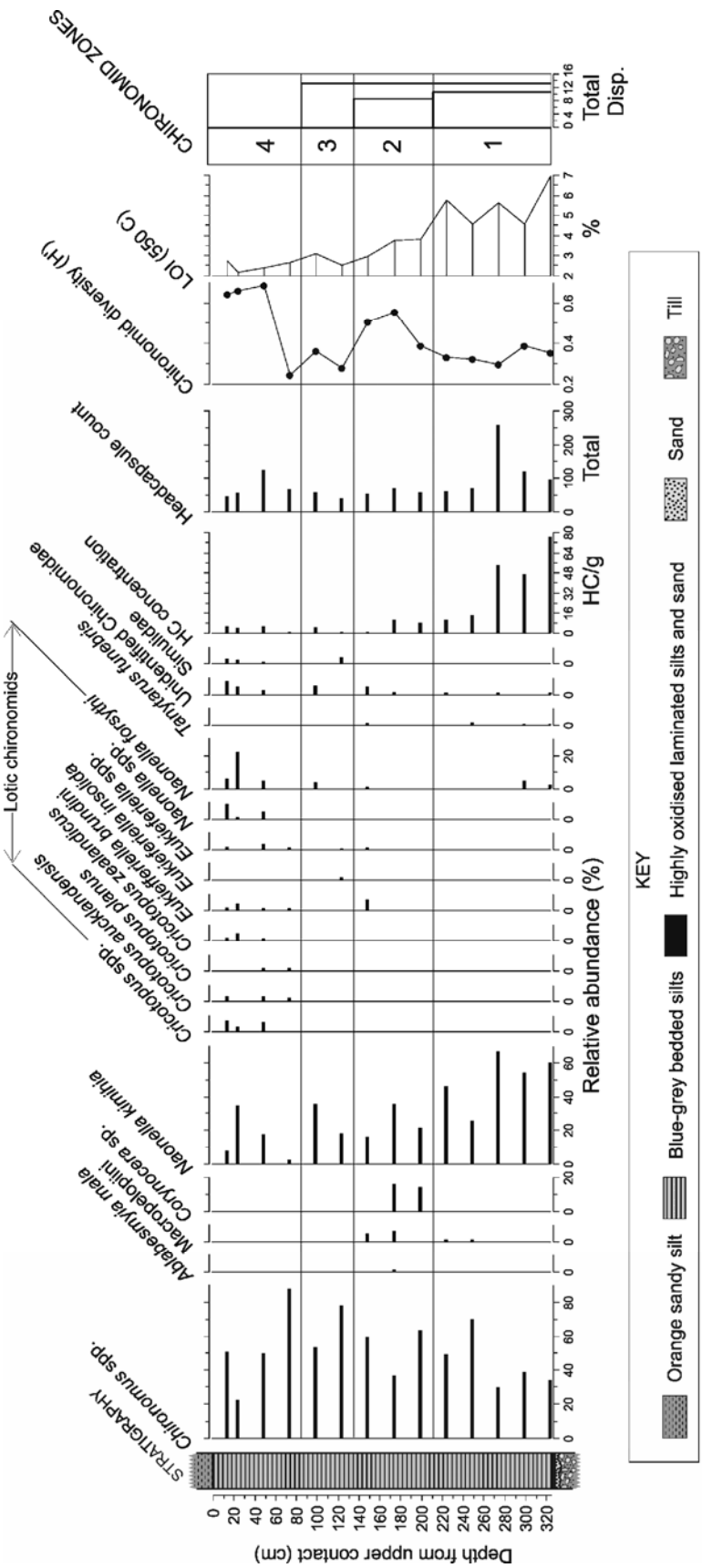


Fig. 7.3: Chironomid percentage diagram from the Lyndon Stream section.

7.4.2. Ordination

A 'time-track' CCA plot of the Lyndon Stream Fossil samples with respect to modern samples and significant environmental variables is shown in **Fig. 7.4**, and with the chironomid zones superimposed in **Fig. 7.5**. Five variables were included as constraining variables in the final CCA in **Chapter 5**: February mean air temperature (Feb Mean), depth, reactive phosphorus (React P), chlorophyll *a* (Chla) and snow. CCA axis 1 is primarily a temperature axis as Feb Mean has the largest absolute canonical coefficient (cc) (-0.594) and the most significant t-value (-4.38) (**Chapter 5**, pp. 43). Depth is also significantly correlated to CCA axis 1, but the significance and explanatory power of this variable is drastically effected by partialling out the effect of Feb Mean. CCA axis 2 is primarily a nutrient/production gradient. Chla is positively correlated with CCA axis 2 (cc = 0.551), while React P is negatively correlated with CCA axis 2 (cc = -0.871). This probably reflects the more limited uptake and utilization of reactive phosphorus in lakes with low biological productivity (Wetzel, 2001).

Changes in ordination space with respect to CCA axis 1 are a direct response of the chironomid taxa to changes in water temperature. In developing the training set all efforts were made to ensure a close relationship between air and water temperature. It is not possible to guarantee that this relationship will hold true in the fossil record, and care should be taken in the interpretation of chironomid-based air temperature reconstructions. There is reason to believe that there have been changes in lake depth, and the input of alluvial material into paleolake Lyndon. I will refer to changes with respect to CCA axis 1 as changes in February mean air temperature, but I will discuss the effect stability of the air/water relationship in the Lyndon Stream chironomid record in **Section 7.5**.

There is a general trend of progressive cooling from the bottom of the section to the top of the section, with a slight warming near the bottom of the record. The cooling signal is overprinted by changes in lake production (chlorophyll *a*) and increasing lake depth. Zone 1 represents a period of slight warming accompanied by an increase in lake production. Zone 2 represents an increase in lake depth and cooling. Zone 3 represents a period of relatively stable temperature and lake depth, accompanied by fluctuations in lake production. Zone 4 represents a period of constant lake depth accompanied by a major temperature decline. This temperature decline is accompanied by a decrease in lake production.

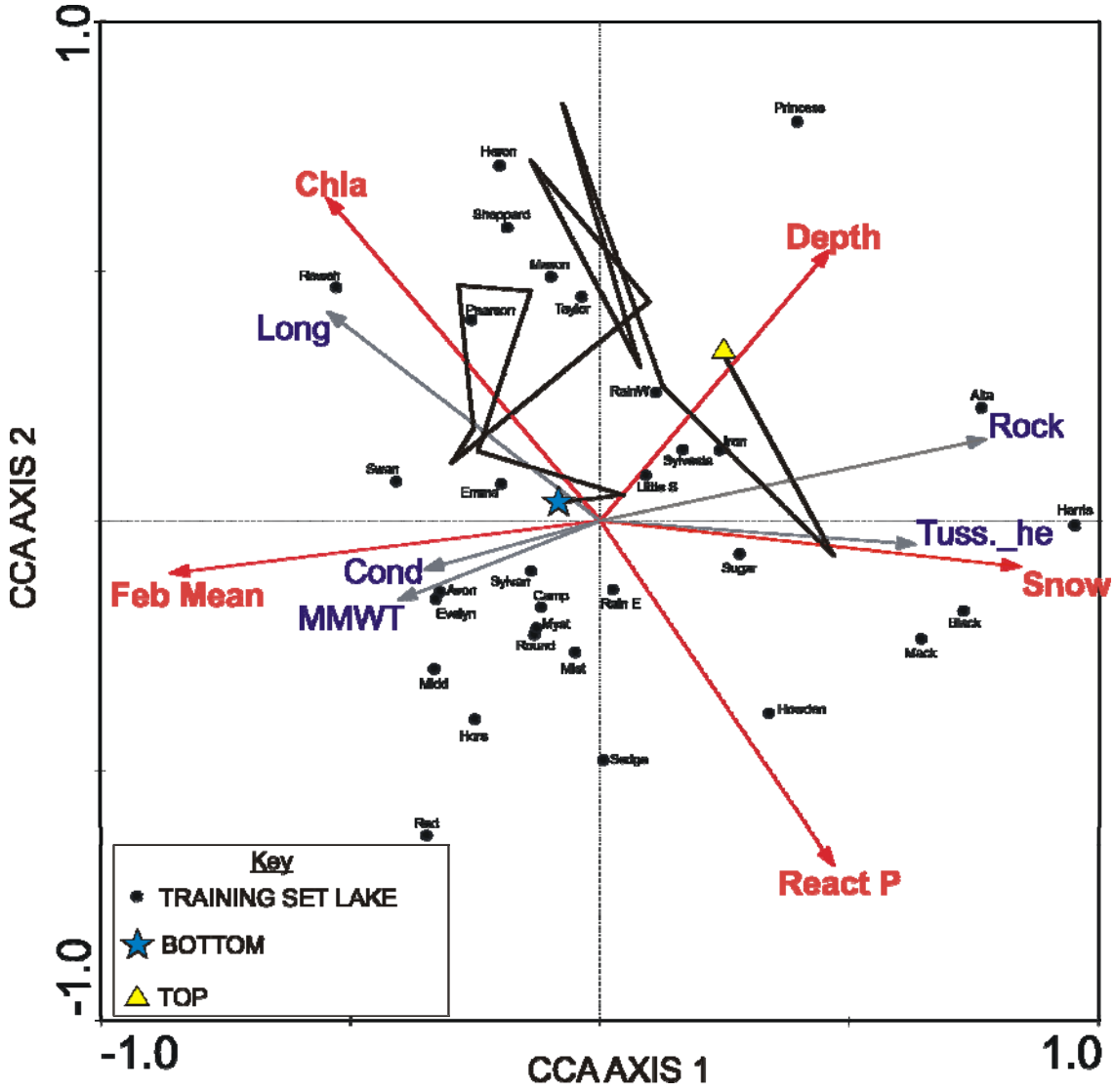


Fig. 7.4: CCA 'time track' plot of fossil samples from Lyndon Stream fitted passively to a CCA bi-plot of the samples from the modern temperature training set with respect to the constraining variables (shown in red) and passive variables (grey arrows, blue text). CCA axis 1 is primarily a temperature gradient, while CCA axis 2 is primarily a production/nutrient gradient. There is a trend of gradual cooling from the bottom to the top of the record accompanied by changes in lake depth and production.

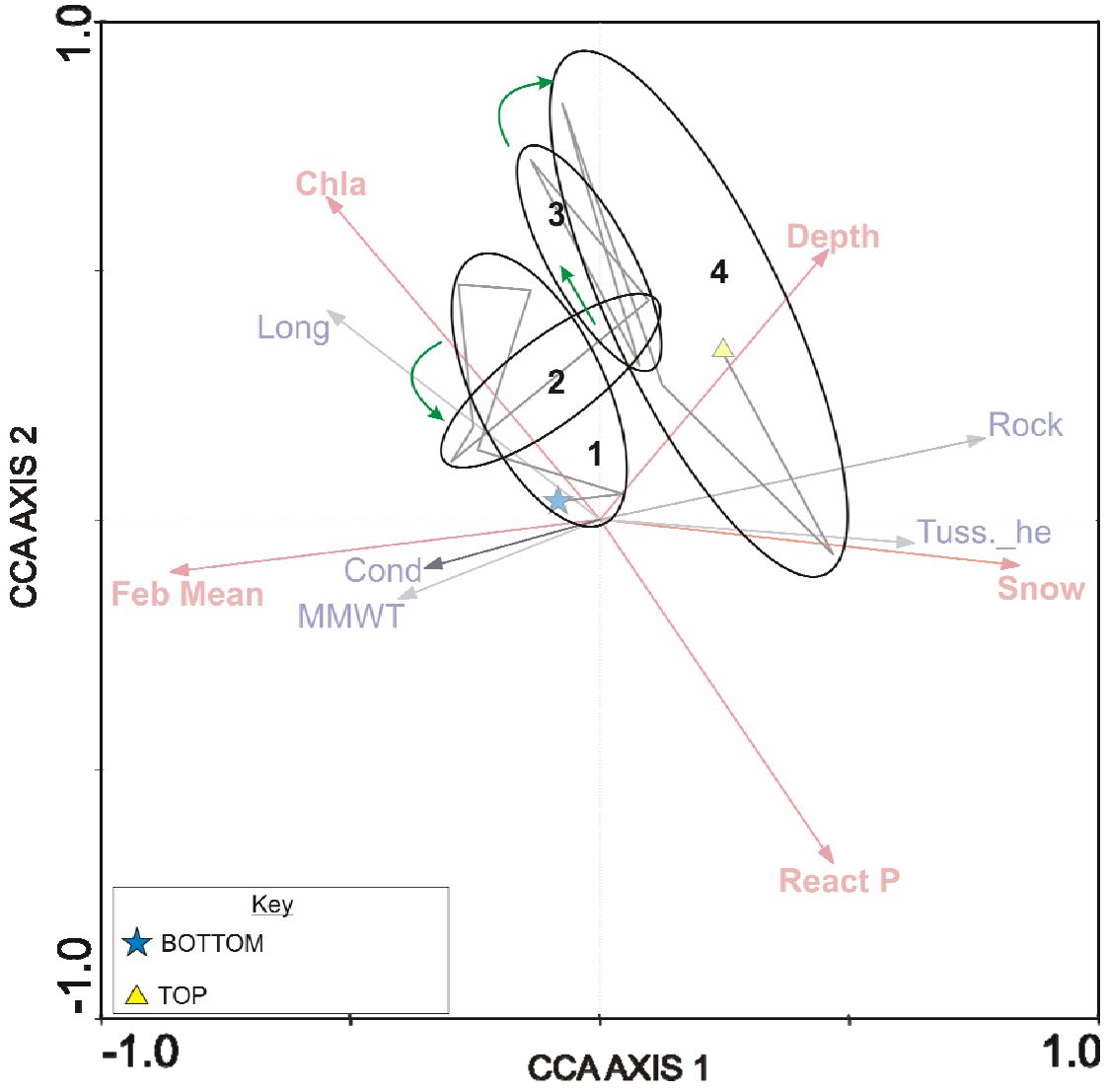


Fig. 7.5: The CCA 'time track' plot of fossil samples from Lyndon Stream from Fig. 7.4 with the chironomid zones (**Fig. 7.3**) labelled. Changes in **Zone 1** appear to reflect increasing lake production (chlorophyll *a*). **Zone 2** represents a period of cooling and possibly an increase in lake depth. **Zone 3** is a period of relatively stable temperature and depth , with fluctuations in lake production. **Zone 4** is a period of major cooling.

7.4.3 Quantitative temperature reconstructions

Chironomid-based February mean air temperature reconstructions using the PLS, WA, and WA-PLS methods are depicted in **Fig. 7.6A**, **B**, and **C**. The temperature reconstructions range between 2 ºC warmer and 3.5 ºC cooler for all three methods. Both the WA and PLS based reconstructions indicate a slight warming in the lower part of the record and an abrupt cooling at the top. A plot of the CCA axis 1 scores (**Fig. 7.6D**) also indicates that chironomid assemblages at the top of the section are typical of cooler high altitude lakes, while those at the bottom of the section are typical of warmer lakes. A LOESS smoother fitted to the WA and PLS temperature reconstructions indicates a slight increase from ca 1 ºC to 0.5 ºC cooler than the modern Feb Mean at the base of the section, with an abrupt cooling between 150 and 210 cm from 0.5 ºC to ca 1.5 ºC in the top 120 cm of the lake sediments. A LOESS smoother fitted to the WA-PLS-based temperature reconstructions indicates that WA-PLS-based temperatures are slightly warmer, with temperatures at the bottom of the section approaching the modern Feb Mean. There is a trend of slight cooling between the base and 120 cm depth, with a slight temperature increase in the top 120 cm.

7.5 Discussion

7.5.1 Ecological interpretation

The evidence from chironomids (this study) and macrophyte remains (Soons and Burrows, 1978) suggest that paleolake Lyndon was a shallow (< 6m water depth) oligotrophic to mesotrophic lake. The remains of *Myriophyllum elatinoides* and *Potamogeton cheesmanii* were particularly abundant in the basal sample described by Soons and Burrows (1978). Although these species are restricted to water depths of < 6m (Clayton et al., 1989), it could also be possible that these sediments were deposited in deeper water if the macrophyte remains were transported from the lake margin. However, the remains of macrophytes that are typical of deeper water (e.g. Charophyceae (Clayton et al., 1989)) were absent from these sediments. Chironomid assemblages at the base of the record in the CCA plot (**Fig. 7.4**) are in the vicinity of Lake Emma and Little Lake Sylvester which have maximum depths of 2.2 and 14m respectively.

The chironomid assemblages from chironomid Zone 3 and 4 are typical of deeper lakes such as Lake Heron, Mason and Taylor (**Fig. 7.4** and **7.5**) which have maximum depths of 37, 36, and 35 m respectively. It appears that chironomid Zone 2 represents a period of increasing lake depth

accompanied by a reduction in water temperature. The remains of *Myriophyllum elatinoides* and *Potamogeton cheesmanii* were not quantified in this study but were observed to be rare in the top 150 cm of the Lyndon Stream section. The organic content of the lake sediments also decreases sharply above 200 cm depth from the upper contact. True laminations were also more common in the lake sediments in the top 150 cm. The absence of shallow water macrophytes and the increased occurrence of true laminations suggests deposition in deeper water.

A reduction in average water temperature would be possible with an increase in water depth, without a reduction in air temperature due to thermal stratification of deeper lakes and the attenuation of solar radiation with depth. This has implications for the air temperature reconstructions that will be discussed in **Section 7.5.2**.

The CCA plots of the fossil samples (**Fig. 7.4** and **7.5**) also indicates changes in lake production (chlorophyll *a* (Chla)). The warming trend at the base of the section indicated by the WA and PLS reconstructions (**Fig. 7.6B** and **C**) is accompanied by an increase in lake production in chironomid Zone 1. At the Zone 1/Zone 2 transition there is a sharp drop in lake production. *Corynocera* spp. and Macropelopini are typical of unproductive lakes in the training set (see **Chapter 5**). *Corynocera* spp. is typical of shallow (< 10m deep) clear lakes (this study, Boubee, 1983). The disappearance of *Corynocera* spp. could be due to an increase in lake depth. The decrease in the relative abundance of *Naonella kimihia* (a littoral taxon (Boubee, 1983)) at the top of chironomid Zone 2 lends support to this theory.

It is not clear why the Macropelopini disappear from the record at the top of Zone 2. The Macropelopini are still abundant in cold (Feb Mean = 11.4 ºC), deep (> 30m) lakes (e.g. Lake Mackenzie) in the modern training set (**Chapter 5**). Extremely low head-capsule concentrations (< 5 head-capsules/g, **Fig. 7.3**) at the top of Zone 2 indicate either a low chironomid larval production or an increased sedimentation rate. The Macropelopini are predatory (Berg, 1995) and feed on other chironomids. If the low head-capsule abundance is indicative of a low chironomid larval production, a lack of food resources could have prevented the survival of the Macropelopini. The Macropelopini may also be capable of switching feeding modes if necessary, and can possibly feed on organic detritus (Berg, 1995). The low organic content of the lake sediments in Zones 3 and 4 suggest that this food resource was also limited.

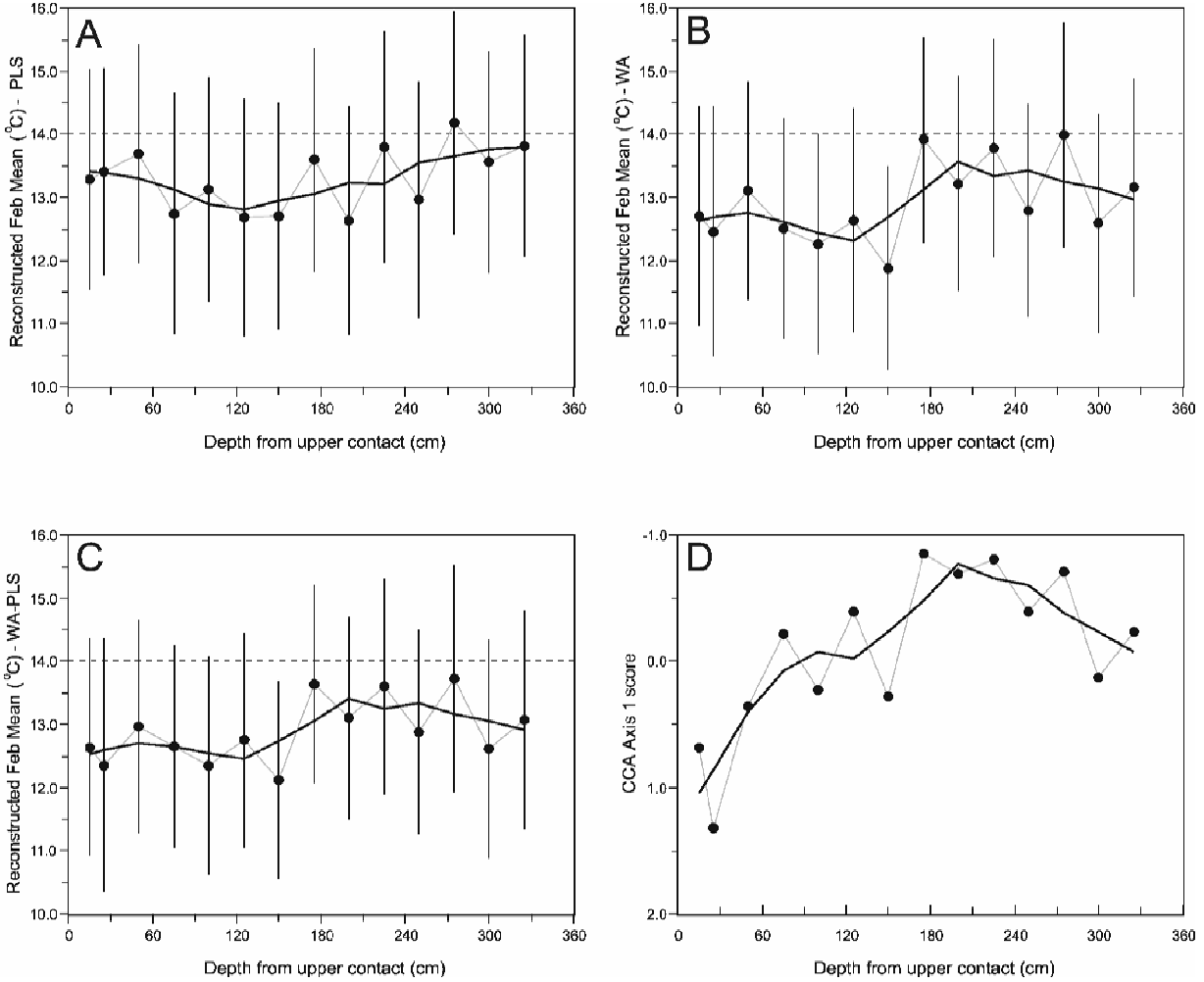


Fig. 7.6: **A**, **B**, **C**. Chironomid-based February mean temperature reconstructions based on PLS, WA, and WA-PLS methods respectively. Horizontal dashed line = modern February mean at the site. Vertical lines = sample specific errors.
D. Plot of CCA axis 1 scores for the fossil samples. CCA axis 1 is a temperature gradient. The y-axis has been reversed so that warmer samples are at the top and cooler samples are at the bottom.

Soons and Burrows (1978) suggest the possibility that the basal lake silts comprised glacially derived sediments, and that the change from lake silts to the coarser orange sandy silts further up-section represents the migration of an alluvial fan into the lake. The migration of an alluvial fan into the lake is supported by the increase in chironomid (and other taxa) that are typical of running water (= lotic habitats) in Zone 4 (**Fig. 7.3**). *Crictocopus*, *Eukiefferiella*, and *Naonella* are common components of New Zealand river macroinvertebrate communities (Milner et al., 2001). The presence of head-capsules from the blackfly *Austrosimulium* (Simulidae), another common taxon in streams and rivers (Collier et al., 1998), also suggests the proximity of this site to a stream or river. There is no chironomid-based evidence for the proximity of ice during the deposition of the lake silts. The absence of the chironomid taxon *Maoridiamesa* in the lotic assemblage (and elsewhere in the record) implies that even though there was possibly a slight cooling mid-section, this site was not close to a glacier face during the deposition of the lake silts (Milner et al., 2001).

Lotic chironomid taxa are also typically cold stenotherms (Pinder, 1995). It was observed that high altitude lakes in the modern training set that were deep (e.g. Lake Harris) or had a high input of snow-melt during the summer (e.g. "Gertrude Saddle") also had high relative abundances of lentic taxa, particularly *Maoridiamesa* or *Naonella forsythi* (**Chapter 5**). It is therefore possible that a reduction in air temperature associated with continued deep-water conditions resulted in a higher relative abundance of lotic taxa. Walker and Mathewes (1989) argue that the scouring of the littoral zone in large deep high altitude lakes, and the cold temperatures at depth, prevent the typical chironomid assemblage of shallow ponds or tarns from successfully colonizing these waterbodies.

It is important to consider these two possibilities when interpreting the chironomid-based temperature reconstructions. The cooler temperatures at the top of the section reconstructed using the WA and PLS based methods could indicate a true cooling or merely an increased influx of head-capsules from lotic taxa as the alluvial fan migrated into the lake. The latter situation would cause an under-prediction of the air temperature. The fact that paleo-lake Lyndon was also deeper at the top of the section adds further complications to the interpretation of the temperature reconstructions. This is discussed in the following section.

7.5.2. Implications for New Zealand LOGS climate conditions.

There are two published radiocarbon ages that constrain the chronology of the lake silts. A basal age of 22,200 +/- 750 ^{14}C yr BP (NZ 3940), and an age from the upper *Sphagnum* silts of 19,200 ^{14}C $\pm$ 550 yr B.P (NZ 4298) (Soons and Burrows, 1978). These radiocarbon ages were calibrated

using INTCAL98 (Stuiver et al., 1998) and yielded ages of 26,651 +/- 1009 cal. yr BP for the base of the silts, and 23,026 +/- 646 cal. yr BP for the upper *Sphagnum* silts. The chironomid record only extends to the top of the lake silts, but there is no radiocarbon age for the top of this unit at present. Therefore an approximate age for the top of the lake silts of 24,500 cal. yr BP was estimated by interpolation. The uncertainty of the basal radiocarbon age (27660-25642 cal. yr BP) suggests the possible existence of the Kawakawa tephra (26,500 cal. yr BP) at the base of the lake silts; this was not seen in the field. I am aware of one luminescence age and one AMS radiocarbon age (unpublished) that may reduce the age range of the base of the lake silts by up to 800 yrs. Further dating of this deposit and confirmation of the presence/absence of the Kawakawa tephra will serve to further constrain the chronology of these deposits, but a mid-LOGS (MIS 3/2 transition) age seems secure.

The chironomid-based temperature reconstructions are in agreement with the beetle-based estimates of Marra et al. (2006) and the macrofossil based inferences of Soons and Burrows (1978) (**Fig. 7.7**). Therefore the chironomid-based temperature model seems to be producing reasonable reconstructions. Marra et al. (2006) inferred a February mean that ranged from 0.5 ºC warmer to 1.9 ºC cooler than the modern February mean from a sample taken at the base of the Lyndon Stream section (**Fig. 7.7**). Soons and Burrows (1978) noted the presence of seeds and pollen from *Potamogeton cheesmanii*, *Montia fontanam* and *Myriophyllum elatinoides* in a stratigraphically equivalent sample. These plants are present up to an altitude 400m higher than the Lyndon Stream locality today. An increase in altitude of this magnitude would be equivalent to a reduction in the February mean of up to 2.5 ºC.

The chironomid-based reconstruction from the same horizon (300 cm depth from the top of the lake silts) inferred a February mean between ca 1 ºC warmer and 2.5 ºC cooler than the modern February mean (**Fig. 7.7**). Therefore, the chironomid estimate falls within the range of temperature reconstructions based on the beetles and macrofossils. Based on all the samples, the chironomid-based reconstruction estimates temperature variations between 1.7 ºC warmer and 3.7 ºC cooler than the modern February mean

I believe that it is highly unlikely that temperatures would have been warmer than the modern February mean at this time. Several warm stenothermic species are absent from the Lyndon Stream lake sediments. *Cladoplema curtivalva* and *Polypedilum* spp. occur in modern oligotrophic to mesotrophic lakes proximal to this study site (Schakau, 1993). Most critically ,the lower temperature limit of *Cladoplema curtivalva* observed in the modern training set was 12.4 ºC (**Chapter 5**). I conclude that if February mean temperatures were above this threshold, *Cladoplema curtivalva*

should be present in the Lyndon Stream record. I therefore suggest a temperature depression of at least 1.6 ºC (**Fig. 7.7**).

Overlapping the temperature inferences from all three proxies (chironomids, macrofossils, and beetles) provides a temperature estimate of between ca 12 and 12.4 ºC which corresponds to a cooling of between 1.6 and 2 ºC relative to the modern February mean for this site (**Fig. 7.7**). This suggests that the chironomid-based temperature inference models are over-estimating the February mean temperature in this instance. The residual plots (**Fig. 6.1**, **Chapter 6**) for all of the temperature inference models (PLS, WA, WA-PLS) reveal that all three models over-estimate air temperatures at the low (< 12 ºC) end of the temperature gradient.

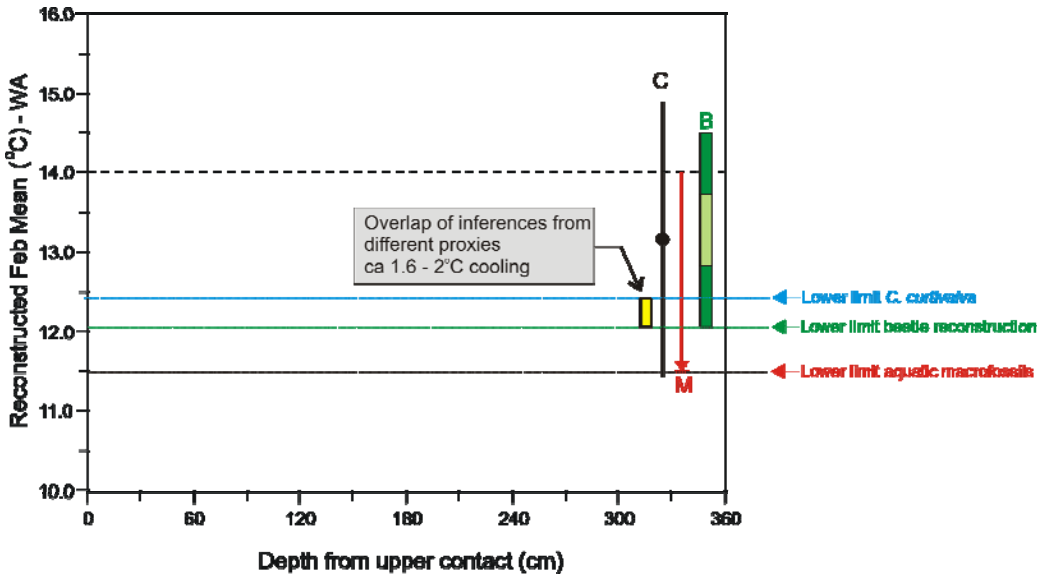


Fig. 7.7: Comparison of the chironomid based (C) macrofossil-based (M) (Soons and Burrows, 1978) and Beetle based (Marra et al.,2006)temperature inferences. The lower observed temperature limit for the warm stenothermic chironomid taxon C. curtivalva (12.4 ºC) is shown. The overlap between the 3 proxies (Beetels, macrofossils and chironomids) is shown as a yellow bar.

The bias for the PLS and WA-PLS methods increased towards the low end of the gradient and was higher (+1.5 ºC) than the WA method (ca +0.6 ºC) at the lower temperature extreme. The lower consistent average bias (ca +0.6 ºC) for the WA method suggests that this method is more suitable for the inference of lower temperature thresholds. Bootstrapping cross-validation resulted in a more extreme inference bias for all three methods. The WA method still performed the best but overestimated the temperature at the lower end of the temperature gradient by 1.2 ºC (**Fig. 7.8**).

Reducing the chironomid-based estimates by 1.2 ºC drops the smoothed reconstructions for the entire record below the lower limit of *C. curtivalva* (**Fig.7.9**). It therefore seems likely that the chironomid-based temperature reconstructions fall in the lower portion of the estimated temperature range provided by the sample-specific errors.

The increase in lake depth, and the migration of an alluvial fan into paleolake Lyndon in the upper part of the section complicates the interpretation of the temperature reconstructions. The smoothed temperature reconstructions from the WA and PLS methods suggest a temperature decline in the upper part of then section. However, a cooling signal could result from an increase in lake depth or an influx of head-capsules from lotic taxa. My impression is that this cooling is real. There is no guarantee that an increase in lake depth alone will always create a cooling signal. Two of the deep (> 30 m) lakes in the temperature training (Lake Heron and Alta, **Fig. 7.8**) set produced temperature inferences that were actually greater than the observed February mean. The temperature decline actually occurs at 150 cm (**Fig. 7.9**). This is approximately at the mid-point of the lake sediments. The fact that the Bayfield 3 glacial advance occurs after the deposition of the Lyndon Stream lake silts (Soons and Burrows, 1978) also provides support for a true cooling trend towards the top of this record.

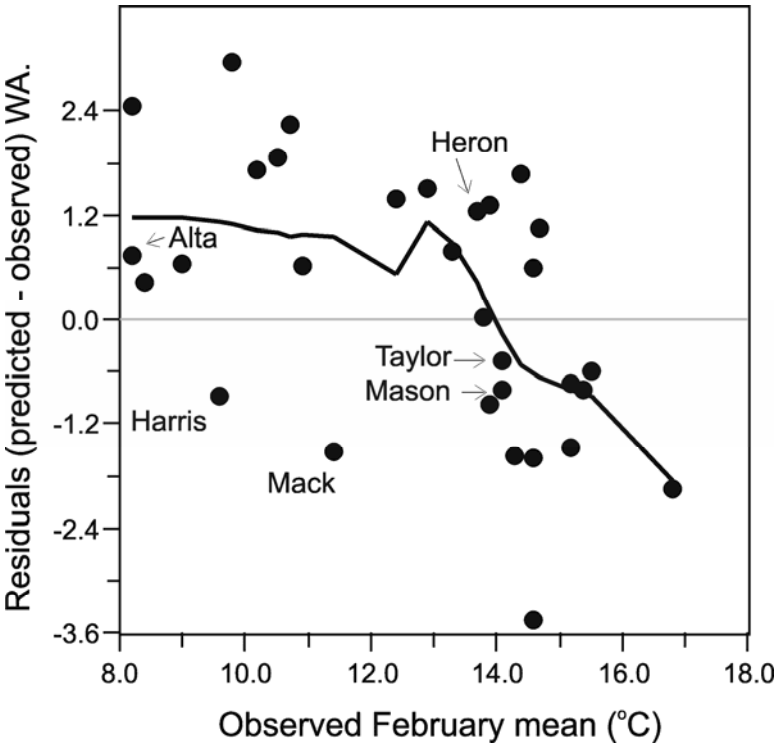


Fig. 7.8: Residual vs observed February mean plot For the bootstrap cross-validated weighted averaging based temperature model. The LOESS smoother has a span 0f 0.45. This model over estimates the cooler temperatures by an average of 1.2 ºC. The position of the deeper lakes (>30m max depth) are shown. Most of these deep lakes produce Temperatures that under-estimate the observed values. Lake Alta and Heron are exceptions to this rule.

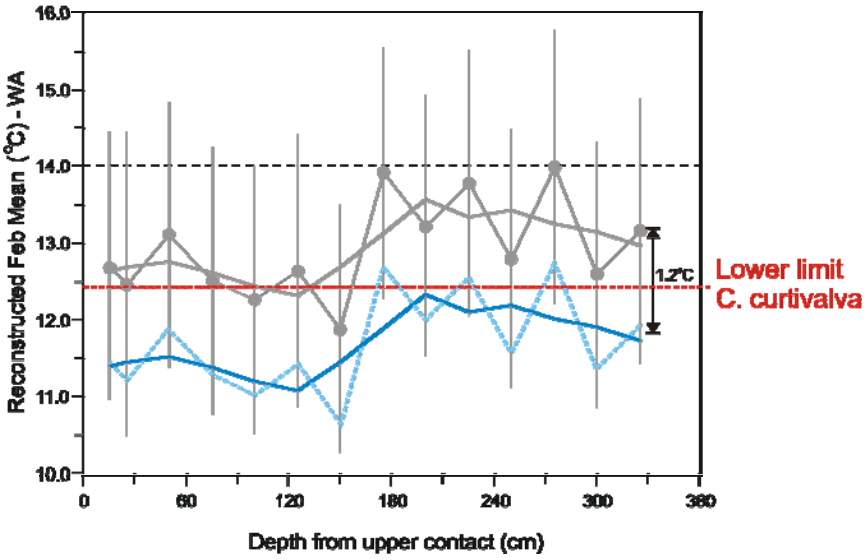


Fig. 7.9: Adjustment of the chironomid-based temperature inferences from the weighted averaging model for the +1.2 ºC average bias in the cooler part of the temperature gradient. The modern Feb Mean at the sight (14ºC) is shown as a horizontal black dashed line.

There is only a minor abundance (ca 5%) of lotic taxa in this horizon, and there is no sedimentological evidence for the inflow of alluvial material. I would also expect that if the head-capsules from the lotic taxa had been washed in from a stream or river, they would show some signs of transport (i.e. damage). The head-capsules from the lotic taxa did not appear to be more damaged than the head-capsules from the lentic taxa.

When calculating the actual decrease in February mean temperature for this period it is necessary to take into account the ca 120m sea-level drop that began ~ 30,000 cal years BP and extended to ~ 19,000 cal years BP (Lambeck et al., 2002). This drop in sea-level would be equivalent to a drop in temperature of ca 0.72 ºC based on a lapse rate of 0.6 ± 0.1 ºC/100 m (Hales and Roering, 2005). This means that the combined data from the beetles (Marra et al., 2006), the macrofossils (Soons and Burrows (1978) and the chironomids infers a cooling of between 0.88 and ~ 1.28 ºC cooler than the sea-level adjusted February mean from the single basal sample. Based on all the samples, the chironomid-based reconstruction estimates cooling between ca 0.88 and 2.98 ºC cooler relative to the sea-level-adjusted February mean.

Soons and Burrows (1978) concluded that the Lyndon Stream lake sediments were deposited during an interstadial, based on the macrofossils and the relationship between the lake sediments and the outwash surfaces associated with the Bayfield moraines (**Fig. 7.1**). The temperature reconstructions from this study and that of Marra et al. (2006) corroborate the interpretation of Soons and Burrows (1978). The absence of a typical ice-proximal chironomid assemblage throughout the section also precludes the presence of glacial ice in the valley at this time. The lake represents an ice free period in this valley between advances and indicates that conditions warmed

up to full or near-full interglacial values. This record confirms the existence of an interstadial in the previously monotonically cold period (~34,000 -18,000 cal yr BP) in New Zealand.

The existence of a significant amount of climate variability during the New Zealand LOGS (including a middle LOGS warming phase) is corroborated by records that are emerging from West Coast sites (e.g. Hormes et al., 2003; Suggate and Almond, 2005; Vandergoes et al. 2005) and the Auckland maar records from the North Island (Sandiford et al., 2001, 2003; Hägg and Augustinus, 2003). Barrows and Juggins (2005) report that the greatest amount of SST cooling (≤ 9 ºC) off the east coast of New Zealand did not occur until the LGM (20,500 ± 1400 cal yr BP (**Fig. 7.10**)). $\delta^{18}O$ records from the Md3 Nettle bed speleothem (Hellstrom et al., 1993) indicate a $\delta^{18}O$ minimum at about the same time as the SST minimum reported by Barrows and Juggins (2005) (**Fig. 7.10**). The timing of the largest peak in the abundance of grass pollen in the Okarito Pakiki pollen record (Vandergoes et al., 2005) also coincides with the timespan for the LGM as defined by EPILOG (2001) (**Fig. 7.10**).

Marra et al. (2004) also performed temperature reconstructions based on beetle fossils from samples ranging from ~ 22,900 to 24,600 calendar years BP from the Awatere Valley in the South Island (**Fig. 7.1** and **7.10**). They inferred a maximum possible temperature decline of ca 5 ºC for February and 6 ºC for July mean temperatures from this site. Therefore, it appears that even though a series of glacial advances began in New Zealand ~34,000 calender years BP, climate conditions were variable and the maximum cooling did not occur until much later at the global LGM.

Many of the pollen records spanning the early part of the LOGS show a climate amelioration shortly after the deposition of the Kawakawa tephra (~ 26,500 cal years BP) (Vandergoes et al., 2005). However, the continued low values (< 20%) of canopy tree pollen (e.g. *Nothofagus*, *Dacrydium cupressinum*, *Podocarpus* spp.) (Moar, 1980; McGlone, 1988; Vandergoes et al., 2005) for the entire LOGS are seemingly at odds with the mild degree of cooling now inferred from the chironomids (this study) and the beetles (Marra et al, 2006) from Lyndon Stream for the middle of the LOGS.

Allowing for the maximum estimated cooling from Lyndon Stream (3.7 ºC) (this study) and a lapse rate of 0.6 ± 0.1 ºC/100 m (Hales and Roering, 2005), the tree-line should drop from its present altitude (~1300m) to ~ 680m asl between 26,600 and 24,500 cal. Therefore large areas of the South Island should have been forested between ~27,000 and 23,000 calendar years BP. The fact that pollen from forest canopy trees remained sparse during the early LOGS suggests that some other environmental factors must have been limiting the growth of forest taxa during this period.

The Lyndon Stream record represents a time period of up to 2000 years. It is possible that a climate amelioration of such a short duration would not allow enough time for the regeneration of the forest cover. However, at the end of the last ice age (~18,000 cal. Yrs BP) the pollen record shows a rapid recovery in the regional vegetation in response to climate change. McGlone et al. (2004) report that the native canopy tree pollen (*Nothofagus*/*Podocarpus*) from Kettlehole Bog (30 km north of the Lyndon Sream site (**Fig. 7.1**)) had reached an abundance of 45% within a thousand years of the last deglaciation.

The chironomids are only capable of reconstructing mean February temperatures, and it is likely that changes in seasonality, mean annual temperature (MAT) and frost frequency may also exert a control on vegetation cover. The beetle based MCR technique is also capable of reconstructing mean July (winter) temperatures (Marra et al., 2006). So far the beetle based mean July temperature reconstructions from Lyndon Stream (Marra et al., 2006) show no significant change in seasonality during this time, with an equivalent amount of cooling (~ 2 ºC) occurring in winter and summer. Further studies investigating the relationship between modern New Zealand pollen assemblages and environmental parameters are required to disentangle the environmental signals represented in the pollen record.

7.6 Conclusions

The mild (< 4 ºC) cooling for the late Otiran glacial sequence between ~ 26,600 and 24,500 cal. yrs BP (MIS 3/2 transition) inferred from chironomids in this study is in agreement with the previous estimates by Soons and Burrows (1978) and the beetle-based estimates of Marra et al. (2006) from the same site. A period of climate amelioration (an interstadial) around this time is supported by other records emerging from other parts of New Zealand (Hormes et al., 2003; Suggate and Almond, 2005; Vandergoes et al., 2005) which indicate ice retreat and a slight recovery in the forest cover.

The apparent inconsistency between the pollen record and the mild conditions inferred from chironomids (this study) and beetles (Marra et al., 2006) during parts of the LGM requires further investigation. The pollen record does show a slight recovery coinciding with the late MIS 3 early MIS 2 ‘interstadial’ but canopy tree pollen is still rare (< 20%) abundances. This fact suggests that environmental parameters additional to temperature are contributing to limit the expansion forest

cover during this time. This study highlights the potential of chironomids based reconstructions to extend and amplify the late Quaternary paleoclimate history of New Zealand.

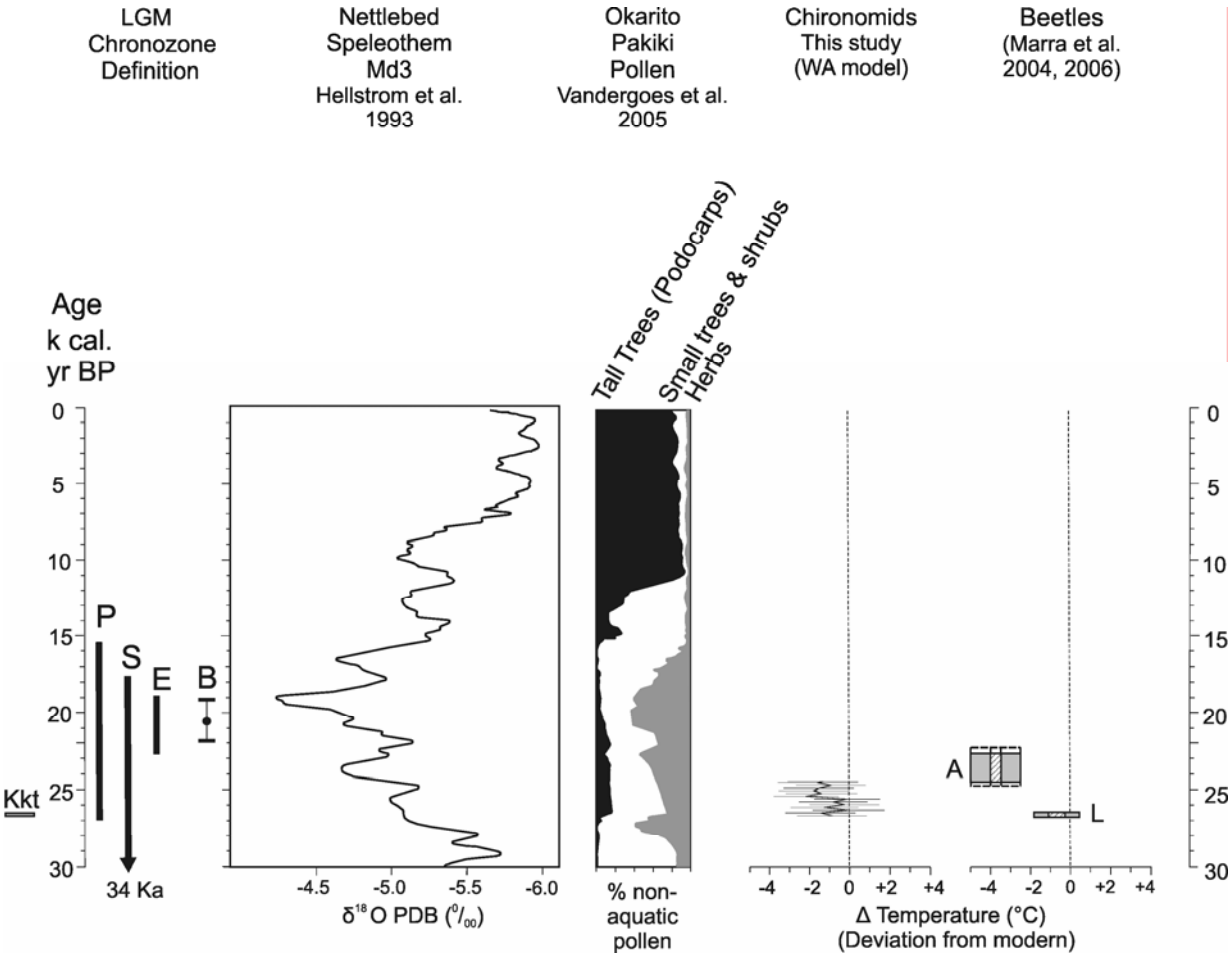


Fig. 7.10: The Lyndon Stream chironomid temperature record placed in context with other paleoclimate proxies.

References are provided for each record. LGM definitions for New Zealand. P = Pillans et al., 1993; S = Suggate and Almond, 2005. E = The global LGM (EPILOG, 2001). B = The sea surface temperature minimum found in LGM records by Barrows and Juggins (2005). Abbreviations for beetle reconstructions: A = Awatere Valley (Marra et al., 2004), L = Lyndon Stream (Marra et al., 2006). Beetle-based February mean reconstructions are shown to allow a direct comparison with the chironomid temperature estimates.

CHAPTER 8: APPLICATION OF THE CHIRONOMID-BASED TRANSFER FUNCTIONS.

PART II: A RECORD OF HUMAN IMPACTS ON THE ECOLOGY AND TROPHIC STATUS OF A KARST LAKE.

8.1 INTRODUCTION

In this chapter I describe the results of a multi-proxy study from a short core taken from a doline lake in the north-west Nelson region in the South Island of New Zealand (**Fig. 8.1 and 8.2**). The principle aim of this study was to test the total nitrogen (TN) transfer-function that was developed in **Chapter 6**. An earlier study of a core from this site (Andrews-Cookson, 2004) revealed a relatively high chironomid taxonomic richness and an abundance of well-preserved macrofossils (e.g. plant material, aquatic invertebrates).

An interview with the land owner also indicated a change in the lake from clear-water conditions to turbid lake-water conditions after the regenerating native forest was cleared from the vicinity of the lake sometime in the early 1970s. This provided me the opportunity to compare the chironomid record from the core samples with historical observations of changes in land-use and lake water quality, and to tie the chironomid-based TN reconstructions to these land-use changes using the plant macrofossils, the pollen record and isotopic dating techniques (e.g. ^{210}Pb).

This study is also significant in that it represents one of only a handful of studies that have investigated the effects of human disturbance on karst environments. Urich (2002) provides an excellent review of the current state of knowledge of the possible effects of various land-use practices (e.g. forestry and agriculture) on the hydrology and ecology in a karst environment.

8.2 SITE DESCRIPTION

8.2.1 Physiography

The study site is a small (0.01 km^2) ~ 18m deep lake located in a tributary of the Takaka River in the north-western part of the South Island, New Zealand (**Fig. 8.1 and 8.2**). The lake bed drops away rapidly from the shoreline, and as a result there is a limited shallow littoral zone and no boggy areas in or around the lake. This lake has no official name, and will therefore be referred

to informally in this text as Alexander Lake, after the local land owner Pat Alexander. The Takaka River catchment ranges in altitude from sea-level to 1859 m (Mount Snowden). 287 km^2 of the total catchment area is mountainous terrain. Mountain ranges include Arthur Range, Anatoki and Snowden Ranges (sub-ranges of the Tasman Mountains) and the Pikikiruna Ranges (**Fig. 8.2**).

The Takaka Catchment lies within the Takaka Terrane, a structurally complex and dismembered belt of Lower Paleozoic rocks (Cooper 1989). The Anatoki Thrust in Northwest Nelson marks the boundary between the Paleozoic Takaka Terrane (eastern) and Buller Terrane (western) (Jongens 1997, Cooper 1989). The Takaka terrane contains a wide range of lithofacies and rocktypes and spans hundreds of millions of years, from Middle Cambrian to Devonian (Roser et al 1996).

The geology of this region is important as it has important consequences for aquifer boundaries, areal and vertical aquifer extent, and influences aquifer development through lithological characteristics. The Arthur Marble aquifer is the primary karst aquifer in this region. This aquifer has an estimated minimum area of 70 km^2 (Mueller 1991). Estimates of the potential cave volume presented by Mueller (1987, 1992) and Williams (1977, 1992) range from 1.5 to 3 km^3.

Alexander Lake is situated in a doline in the Arthur Marble. It could therefore possible that this lake receives water transmitted from the greater recharge zone of the WAM (**Fig. 8.2**). A close inspection of the hydrogeology in the immediate vicinity of Alexander Lake reveals that this is unlikely. The lake is situated adjacent to a major loss zone for the Takaka River (Mueller, 1992) (**Fig. 8.3**). This is an area where the Takaka River flows directly over the unconfined Arthur Marble aquifer, and water is lost from the river to the aquifer. This loss-zone occurs at an altitude of ca 20m asl, and is < 2 km to the east of Alexander Lake. A positive flow from the Takaka River to the aquifer indicates that the river is perched above the water table (**Fig. 8.3**). Alexander lake is located at ca 80m asl so it is likely that this lake is also perched above the water-table. There is no stream flowing directly into the lake itself, although Dry Creek and Stony Creek flow from the upper reaches of the catchment into the Takaka River (**Fig. 8.2**). Thus the lake receives water in the form of overland flow during storm events, continuous throughflow and subcutaneous flow in the upper fractured permeable zone in the Arthur Marble (**Fig. 8.3**). This water is sourced in the immediate catchment of Alexander Lake which is covers an area of approximately 10.5 km^2. Sometime after 1970 an outlet channel was dug to allow water to be drained off for irrigation purposes (P. Alexander (farm owner), pers. comm.). This does not appear to have had a major effect on the lake level.

8.2.2 Climate and vegetation

The Takaka Catchment can be broadly divided into two main climate zones. The cool-wet coastal and cool humid central valley sections are characterised by average to high sunshine hours, and rare frosts in winter. The mountainous terrain of the eastern and western ranges experiences more variable and severe climatic conditions, and commonly incurs snowfalls in winter (Bruce 1987). Mean annual rainfall ranges from a maximum of 5140 mm in the ranges to the west of the catchment to a minimum of 1542 mm on the coast of Golden Bay. The major drivers of precipitation variation are altitudinal variation within the catchment, and the orographic effect of the western ranges.

The vegetation of many of the western sub-catchments of the Takaka River is relatively un-modified and comprises native beech (*Nothofagus*), podocarps (e.g. *Podocarpus*, *Prumnopitys*, and *Dacrydium cupressinum*) or mixed podocarp-beech stands depending on aspect, drainage and soil fertility. At higher altitudes (~ 600m asl) there is a transition to upland beech forest which comprises *Nothofagus menziesii* and *N. fusca* (Wardle, 1984). Eastern catchments and the main valley floor have been heavily modified by human activity (**Fig 8.2**). The vegetation cover now comprises scrub (*Coprosma*, and *Leptospermum*), exotic trees (e.g. *Pinus radiata*), and introduced pasture grasses (e.g. *Pennisetum clandestinum*). Deforestation by Polynesians (1200-1400 AD (McGlone and Wilmshurst, 1999) was more limited in the north-west Nelson region than many other parts of New Zealand and the majority of the human impact on the local vegetation occurred after 1840 following European settlement (Andrews-Cookson, 2004).

The vegetation in the immediate vicinity of Alexander Lake was cleared for pastoral farming in the early 1970s, while some areas to the north and west of the lake were cleared sometime before this (P. Alexander, pers comm.) (**Fig. 8.1** and **8.2**). Much of the lower reaches of the catchment were probably cleared soon after arrival of European settlement but have started to regenerate into a mixed beech (*Nothofagus truncata*)/ podocarp forest (*Dacrydium cupressinum*, *Prumnopitys taxifolia*, *Podocarpus* spp.). The upper reaches of the catchment still comprises un-disturbed beech (*Nothofagus*) forest and much of the lower reaches still comprises regenerating beech/podocarp forest (**Fig. 8.1**). There is a patch of regenerating native forest on the south-western side of the lake (**Fig 8.1**) that includes native canopy trees (e.g. *Podocarpus totara*, *Dacrydium cupressinum* seedlings) and native scrub (e.g. *Leptospermum scoparium*) around the edge of the lake. There are also exotic trees within this patch (e.g *Pinus* spp.) and around the periphery of the lake as well as exotic scrub (e.g. *Ulex europaeus* and *Rubus fruiticosus*) and *Pteridum esculentum*.

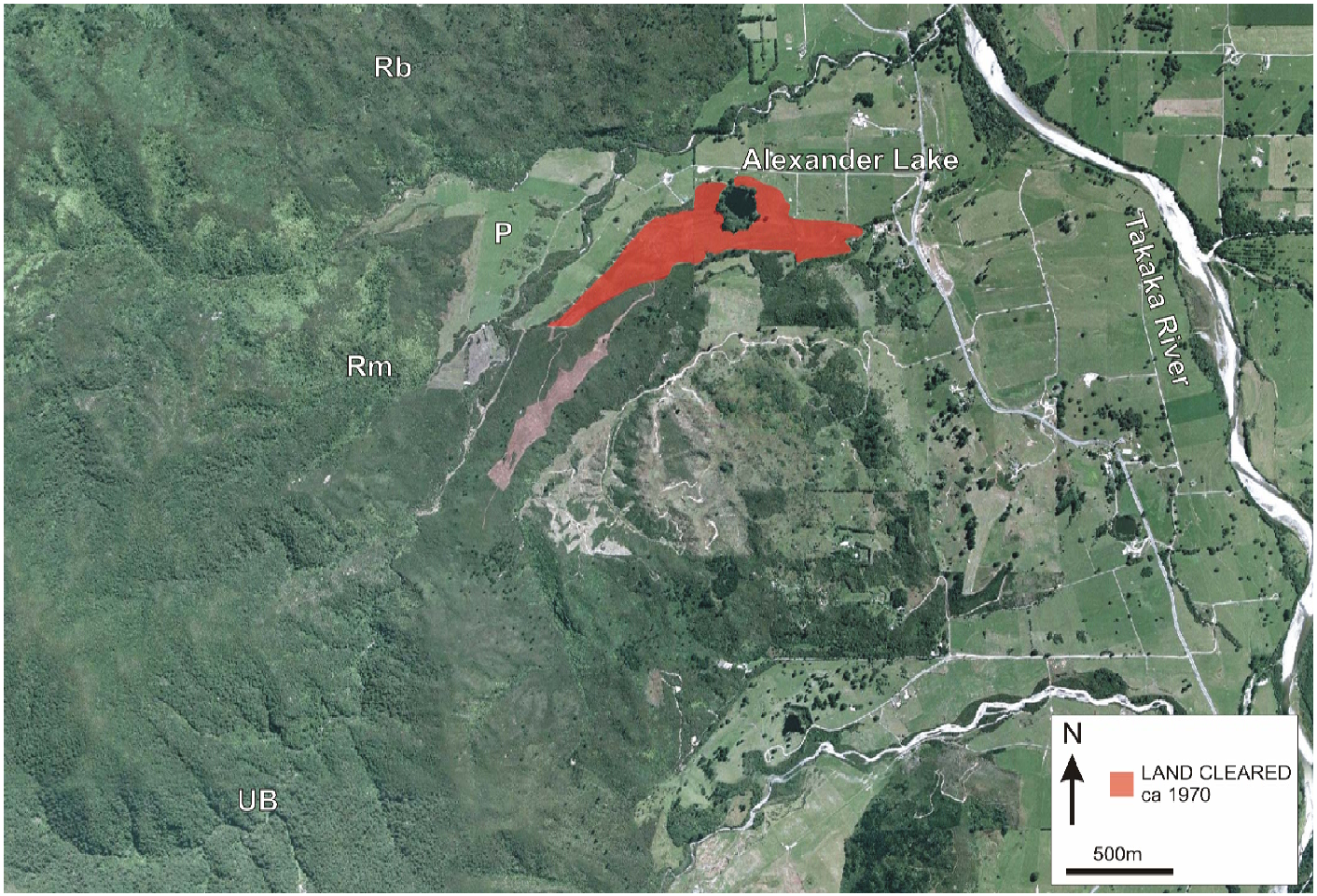


Fig. 8.1: Aerial photograph of the Alexander Lake catchment and the Takaka River valley floor. The area in the immediate vicinity of the lake that was cleared ca. 1970 is depicted. The other areas of pasture to the north and west of the lake were cleared sometime before 1970. Rb = regenerating beech forest. Ub = undisturbed beech forest. Rm = regenerating mixed beech/podocarp forest. P = pasture.

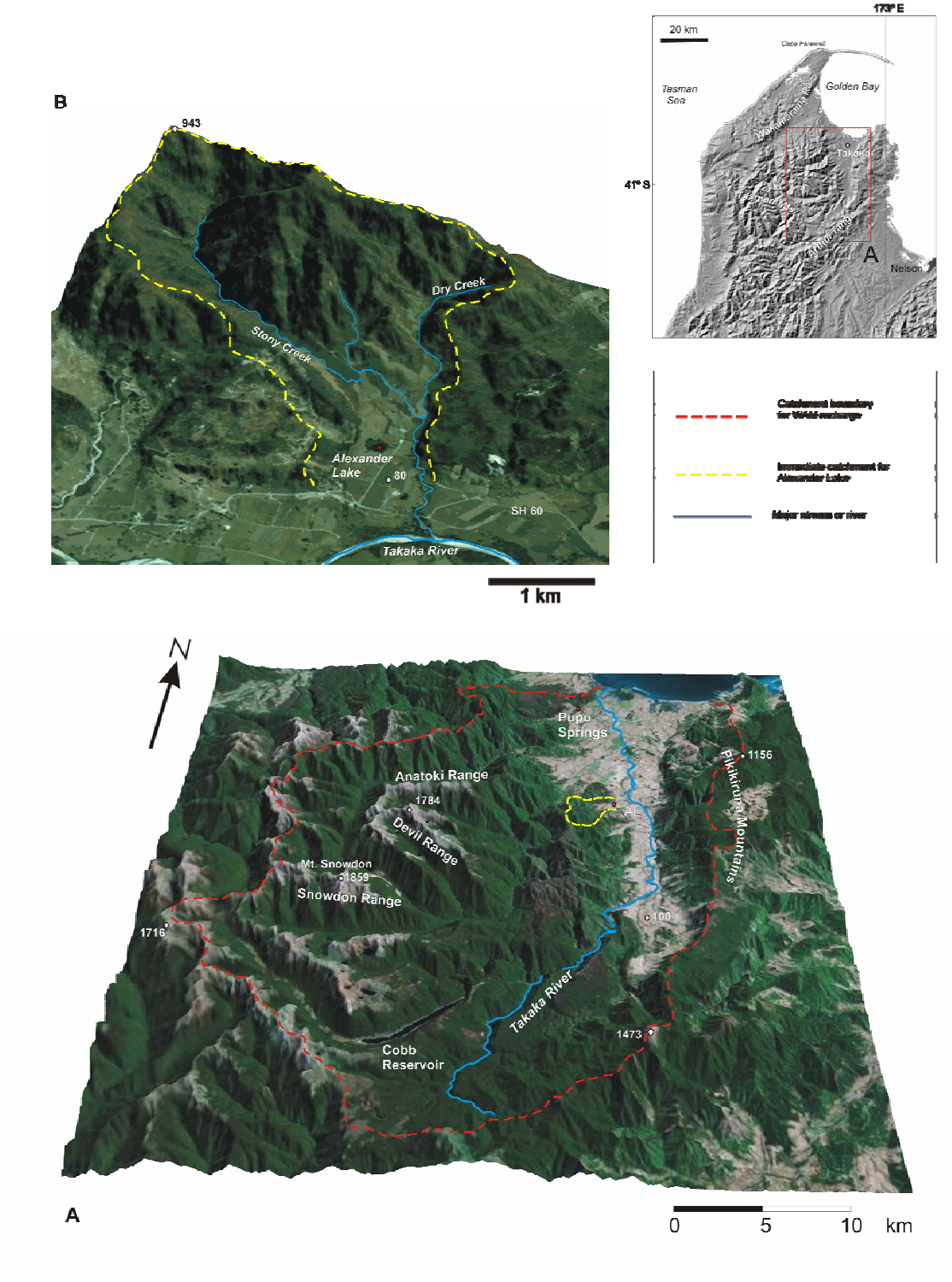


Fig. 8.2: The location of Alexander Lake. **A.** The location of the Takaka River catchment (red dashed lines), which is also the catchment for the local aquifer systems. The immediate catchment for Alexander Lake (overland flow) is shown as a yellow dashed line. **B.** View of the Alexander Lake catchment from the East. The Loss-zone for the Takaka River is in the foreground.

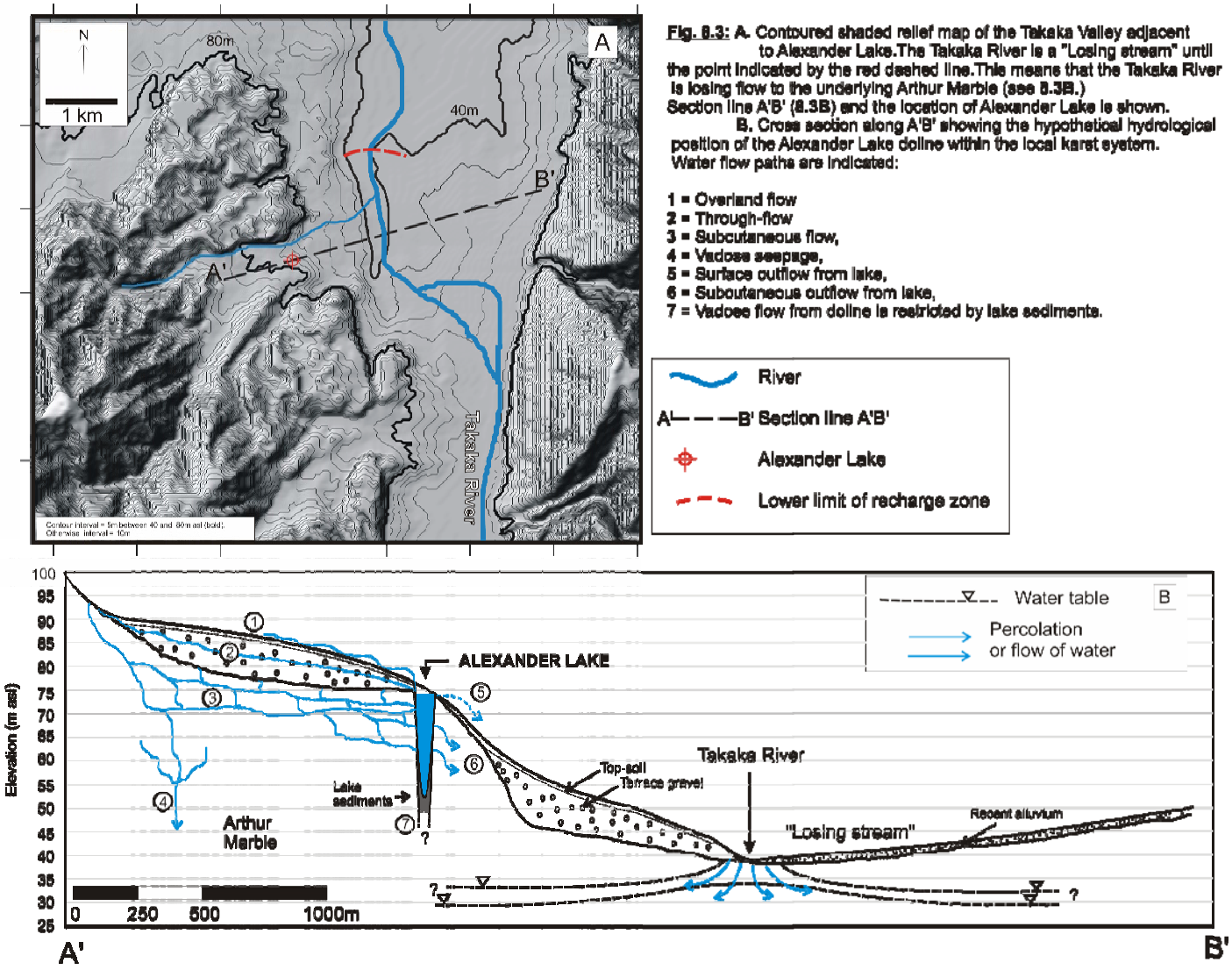


Fig. 8.3: A. Contoured shaded relief map of the Takaka Valley adjacent to Alexander Lake.The Takaka River is a "Losing stream" until the point indicated by the red dashed line.This means that the Takaka River is losing flow to the underlying Arthur Marble (see 8.3B.) Section line A'B' (8.3B) and the location of Alexander Lake is shown.
B. Cross section along A'B' showing the hypothetical hydrological position of the Alexander Lake doline within the local karst system. Water flow paths are indicated:

1 = Overland flow
2 = Through-flow
3 = Subcutaneous flow,
4 = Vadose seepage,
5 = Surface outflow from lake,
6 = Subcutaneous outflow from lake,
7 = Vadose flow from doline is restricted by lake sediments.

8.3 METHODS

8.3.1 Core extraction and analysis

Three short (<16cm) gravity cores (AL-1, 2, and 3) were taken from the deepest point of Alexander Lake. Cores were far enough apart to prevent sampling of sediments that were disturbed by the removal of other cores. The sediment was extruded from the gravity sampler on-site at 1 cm intervals and stored as sub-samples in sealed plastic bags until the laboratory analyses could be performed.

Material from two of the cores (AL-1 and AL-3) was necessary to provide enough material for pollen analysis, macrofossil analysis (including chironomids) and isotopic dating. Each core was described on-site using the Troels Smith (1955) system for the classification of organic sediments and inspected for evidence of sediment disturbance. Correlation between AL-1 and AL-3 was based on loss-on ignition curves (**Fig. 8.4**) and visual comparison.

Small (< 0.5 cc) sub-samples were taken from all samples from AL-1 and 3 for determination of the organic content (loss-on-ignition (LOI)) following the methods outlined in (Heiri et al., 2001). Samples were weighed wet, and then dried overnight to remove excess moisture. Samples were then weighed then ashed at 550 ºC for 8 hours, and then re-weighed to determine the loss-on-ignition.

1 cc and 2cc sub-samples were also taken from each cm interval from AL-3 for pollen and chironomid analysis respectively. The methods for the analysis of these samples are outlined in **Chapter 3**, section **3.24** (pp. 34). All of the material from AL-1 was processed for isotopic analysis (^{210}Pb, ^{137}Cs, and ^{239}Pu). Samples were dried for several days, and powdered using a mortar and pestle. The samples were then weighed and sent to Dr Uwe Reiser at Victoria University, Wellington, New Zealand for analysis.

The radionuclide ^{226}Ra is commonly found in rocks and sediments and decays via its daughter product ^{222}Rn (half life 3.8 days) to ^{210}Pb (half life 22.3 years). In a sediment older than c. 150 years, the ^{210}Pb will be in equilibrium with its ancestor ^{226}Ra (i.e., "supported ^{210}Pb"), assuming no losses via ^{222}Rn diffusion. ^{222}Rn is also found in air and is decaying continuously to ^{210}Pb. ^{210}Pb is deposited from the air into lake-water where it attaches to silicate particles which are settling in lakes. The ^{210}Pb deposited from the air gives rise to excess ^{210}Pb in the lake sediments compared with the amounts of ^{226}Ra present (i.e., "un-supported ^{210}Pb"). It should therefore be possible to estimate the rate of sedimentation from a profile of the un-supported ^{210}Pb activity, particularly the way in which it decreases with depth. It should be possible to estimate the rate of sedimentation if the rate of supply of ^{210}Pb is constant (Appleby & Oldfield 1978).

Ideally ^{210}Pb activity decreases to a constant value at depth, which is assumed to be a constant background to be subtracted from the ^{210}Pb activity at the surface of the profile. If the ^{210}Pb deposition rate is constant, a log-linear profile of activity vas depth should be found (Whitehead et al., 1998). The time for a 50% decrease in activity, caused by the decay of ^{210}Pb should correspond to 22.3 years, which is the half-life of this nucleotide. Deviations from this log-linear profile can be caused by sediment disturbance, or changes in the rate of ^{210}Pb influx, i.e. increases or decreases in the rate of allogenic sedimentation (Whitehead et al., 1998). A decrease in the input of allocthonous material into a lake (i.e. a reduced sedimentation rate) will lead to an increase in the activity of unsupported ^{210}Pb.

Both ^{137}Cs and ^{239}Pu are a by-product of the atmospheric testing of nuclear weapons. Contamination of the atmosphere by the by-products of nuclear testing began in 1945 with the first above-ground weapon test in the USA. The last above-ground test was conducted in China in 1980 (Matthews, 1995). Appreciable concentrations of ^{137}Cs were not detected in New Zealand rain-water until 1953, and peaked in 1965 (Whitehead et al. 1998). The 1965 peak is the result of high-yield weapons tests by the USSR and USA in 1961 and 1962. The rapid decline in the concentration of ^{137}Cs after 1965 was followed by a minor increase between 1966 and 1974 that was the result of nuclear testing by France at Mururoa. There was no detectable effect on the ^{137}Cs concentration in New Zealand from the Chernobyl reactor explosion of April 1986 (Matthews, 1995).

8.3.2 Data analysis and presentation of results

The abundance of each chironomid taxon was expressed as a percentage of the total head-capsule count for each individual horizon. Pollen abundances were expressed as the percentage of dryland taxa from the dryland pollen sum (total pollen sum minus aquatic taxa). The abundance of common macrofossils (e.g statoblasts) was expressed as concentrations per g of dry sediment.

Taxon abundances were displayed relative to stratigraphic depth using the computer program C2 (Juggins, 2003) for the chironomids and Psimpoll 3.10 (Bennett, 2002) for the pollen diagram. Zonation of both the chironomid and pollen records was based on a visual inspection of both diagrams separately. Zones were assigned to horizons where changes in abundance of many taxa or common taxa occurred.

Total nitrogen (TN) concentrations were reconstructed using the best selected WA-PLS, PLS, and WA transfer-functions (see **Chapter 6**) using the computer program C2 (Juggins, 2003).

Bootstrapping cross-validation was applied to each model to allow the construction of sample specific errors.

Transfer-functions were tested on the modern training set using both unimodal (WA-PLS and WA) and linear methods with all of the taxa that were abundant >2% in at least 2 lakes (2% deletion) (16 taxa) and only those taxa that displayed a significant response to TN (6 taxa) as tested in **Chapter 6**. The performance statistics for these inference models were re-examined because bootstrapping cross-validation was necessary to construct the sample specific errors. The best models were selected based on the r^2, the sample specific errors and whether each model under- or over-predicted the TN concentrations at the upper or lower end of the TN gradient.

8.4 Results

8.4.1 Stratigraphy and chronology

Stratigraphy

The two cores (AL-1 and AL-2) were divided into 6 and 8 units respectively. The subdivision of the cores into these units was based on the Troels Smith (1955) sediment description (**Fig. 8.5**). The top 2 cm of both of these cores consisted of a light green deposit that comprised un-decomposed (*humositas* 0) unidentified algae. Preliminary examination of this horizon revealed that macrofossils were extremely sparse.

AL-1: This core was 14cm long.

Unit 1. Basal unit, 7-14 cm. Ld^{1}, Sh^{2}, Dl^{1}. A dark brown sediment (nigor 4) with abundant remains from lignous plants (*Detritus lignosus* (Dl)) (leaf fragments, seeds, etc.). Organic content (LOI) gradually decreases from the base of this unit (ca 60%) to the top (30%). The contact with the overlying unit was gradational.

Unit 2. 6-7 cm. Ld^{2}, Sh^{2}, Dl^{+}. This sediment unit was a slightly lighter shade of brown (*nigror* 3) due to a reduction in the abundance of the remains of lignous plants (Dl). The organic content (LOI) is ca 25%. The contact with the overlying unit is gradational.

Unit 3. 5-6 cm. Ld^{2}, Sh^{1}, As^{1}, Dl^{+}.

Unit 4. 4-5 cm. Ld[1], Sh[1], As[2], Dl[±].

Unit 5. 3-4 cm. Ld[2], Sh[1], As[1], Dl[±]. These 3 units represent a gradual reduction then increase in organic content between 4 and 6 cm. LOI decreases to a minimum of ca 10% between 4 and 5 cm (Unit 4), and then increases slightly between 3 and 4 cm (Unit 5). The sediment is a pale grey-brown with a low abundance of Dl.

Unit 6. 2-3 cm. Ld[3], Sh[1], As[±], Dl[±]. A light brown, aqueous lake mud (gyttja) with a low abundance of Dl.

AL-3: This core was 16cm long. Units 3-8 appear to be correlated to Units 1-6 in AL-1. These units are compositionally identical. This correlation was also based on the sharp reduction in LOI in both cores at 6 and 7 cm in AL-1 and AL-3 respectively (**Fig. 8.4**). This correlation is also supported by a peak in the concentration of ^{210}Pb between 7 and 8 cm in AL-1 and a peak in the pollen concentration between 8 and 9 cm (**Fig. 8.4**) (see discussion in **Section 8.5.1**). Units 1 and 2 in AL-3 differed from Unit 3 because of the high concentration of wood fragments (*Trunci et rammi*) in these horizons. The matrix containing the large (> 1 cm ∅) wood fragments in AL-3 was identical in composition to unit 3 from AL-1. The LOI measurements depicted in **Fig. 8.4** were based on samples from this matrix.

Chronology

Because of the large amount of material required, it was only possible to obtain isotopic data from AL-1 (**Fig. 8.4**). However, correlation between AL-1 and AL-3 appears to be straightforward, and represents an offset of 1 cm between the two cores (**Fig. 8.4**).

The activity of both ^{137}Cs and ^{239}Pu peaks at 8.5 cm depth. ^{137}Cs is present with activities of at least 6 Bq/kg for all of AL-1, whereas ^{239}Pu is absent from the basal sample (13-14 cm) and top-most sample (2-3 cm) of AL-1. The ^{210}Pb activity decreases from ca 60 Bq/kg between 2 and 3cm to ca 6 Bq/kg between 4 and 5 cm. There is a peak in the activity of ^{210}Pb between 7 and 8 cm (ca 108 Bq/kg) followed by a decrease to ca 24 Bq/kg between 9 and 10 cm. The activity of ^{210}Pb remains at ca 24 Bq/kg to the base of the core.

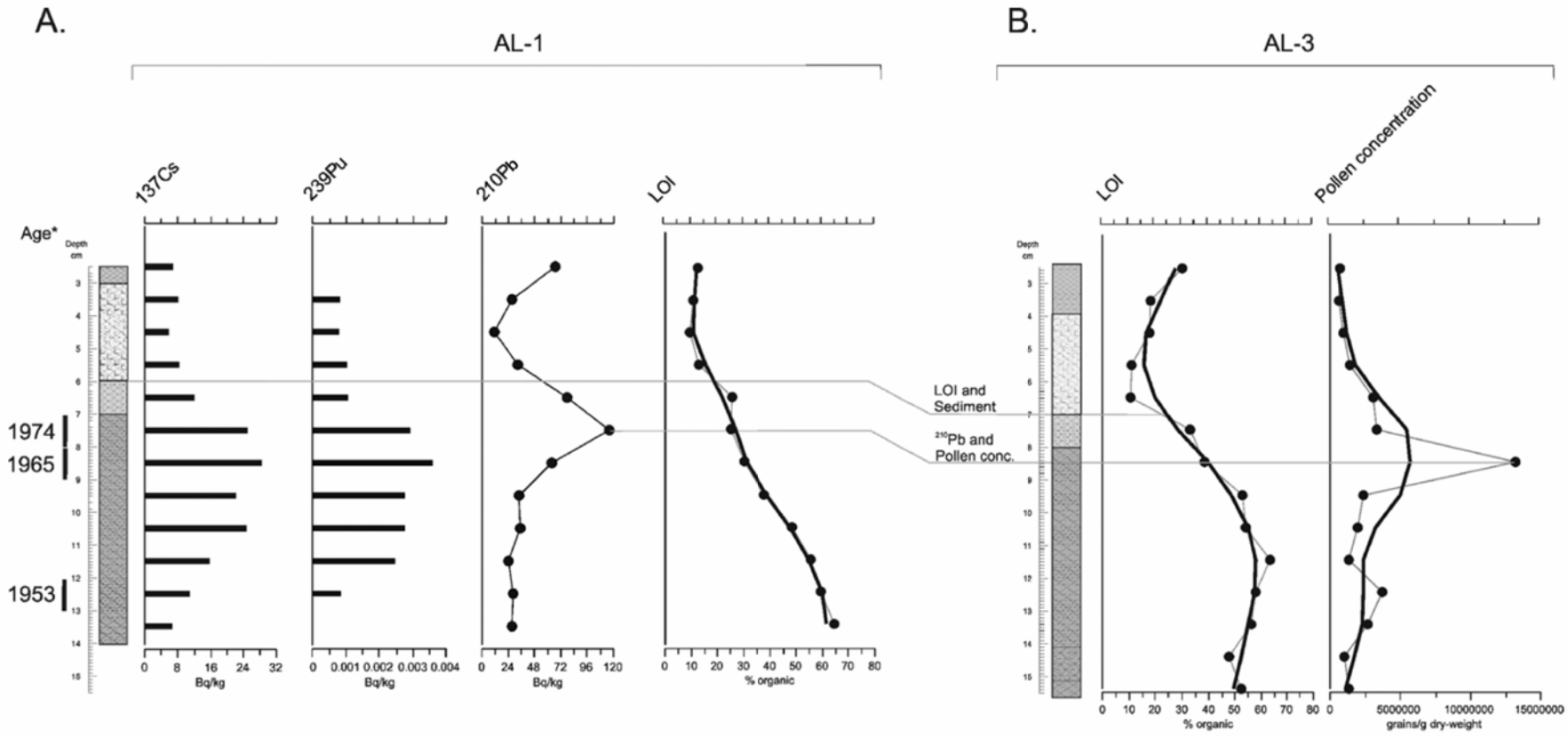


Fig. 8.4: **A.** Troels Smith (1955) sediment description, isotopic profiles (^{137}CS, ^{239}Pu, and ^{210}Pb), and organic content (Loss-on-ignition (LOI)) for AL-1.
B. Troels Smith (1955) sediment description, organic content (LOI) and pollen concentration for AL-3.
Correlation between the two cores is based on the sediment description, the LOI, and the peak in ^{210}Pb and pollen concentration. Such a peak in the ^{210}Pb and the pollen concentration represents a period of reduced sedimentation. Key to sedimentary stratigraphy is provided in **Fig. 8.5C**

8.4.2 Pollen

Pollen grains belonging to 73 morphotypes (including genera, species, and undifferentiated types) were enumerated from 14 samples taken from AL-3 (**Fig. 8.5**). Pollen grains belonging to the *Nothofagus* Fuscaspora type were the most abundant, with relative abundances between 10 and ~ 40 %. Pollen belonging to *Dacrydium cupressinum* was also common in the bottom 7 cm of the core, with abundances decreasing towards the top. Pollen belonging to *Pinus* spp. was most abundant (up to 40%) in the upper 9 cm of the core.

Pollen and spores from aquatic and swamp taxa (monolete ferns and cyperaceae) were rare in AL-3 and comprised < 1% of the total pollen and spore count.

The pollen concentration fluctuated around 25 X 10^5 grains/ g of sediment for the basal 6 cm of the core, with a peak of ~ 125 X 10^5 grains/ g of sediment between 8 and 9 cm. The pollen concentration decreased to < 125 X 10^4 grains/ g of sediment at the top of the core (**Fig. 8.5**).

The pollen record was divided into two Zones (A and B) and two sub-zones (B1, B2) based on the relative abundances of the various pollen morphotypes.

Pollen Zone A. *Nothofagus*/*Dacrydium* zone (9 – 16 cm): The pollen assemblage is dominated by approximately constant abundances of *Nothofagus* Fuscaspora type (~ 40%) and *Dacrydium cupressinum* (~ 20%). There were also low (< 5 %) abundances of *Nothofagus menziesii* and *Leptospermum*/*Kunzea* pollen. Pollen from *Pinus* spp. and the Poaceae is present in low (<2%) abundances. Pollen belonging to native canopy trees comprises 80% of the dryland pollen sum.

Pollen Zone B. *Pinus*/Poaceae zone (2 – 9 cm): There is an increase in the abundance of pollen belonging to the Poaceae and *Pinus* spp. to ~ 10 and 30% of the pollen sum respectively at the top of this zone. The abundance of pollen belonging to *Dacrydium cupressinum* and *N.* fuscaspora-type decreases to ~ 10 and 20% (respectively) of the pollen sum at the top of this zone. The abundance of native canopy tree pollen declines to ~ 20 % at the top of this zone.

Pollen Zone B was sub-divided into two Zones:

Pollen Zone B1. *Poaceae*/*Pinus*/*Pteridium* Zone (4 – 8 cm). Pollen belonging to the Poaceae continue to increase and fluctuate around 5 % of the pollen sum for all of this sub-zone. The abundance of pollen from *Pinus* spp. fluctuates around 10% of the pollen sum. The relative abundance of spores belonging to *Pteridium esculentum* increases sharply at the base off this sub-zone and peaks around 5% of the pollen sum near the top. The abundance of *N. Menziesii*

decreases from ~ 5 % of the pollen sum in Zone B1 to less than 1 % at the top of this sub-zone. The abundance of *D. cupressinum* and *N.* fuscaspora-type fluctuate around 10 and 30% of the pollen sum respectively. The abundance of native canopy tree pollen initially falls to ~ 50% of the pollen sum. Subsequently, there is a slight increase in the abundance of native canopy tree pollen to a peak of ~ 70% between 5 and 6cm. The abundance of native canopy tree pollen declines at the top of this zone to 50% of the pollen sum.

Pollen Zone B2. *Pinus*/Poaceae Zone (2 – 4 cm). The abundance of *Pinus* spp. increases to ~ 40% of the pollen sum, the highest abundance for the entire core. The abundance of pollen belonging to the Poaceae remains constant at about 10%. The abundance of *D. cupressinum* pollen remains low (~ 10%), while the abundance of *N.* fuscaspora-type pollen decreases from ~ 30 to 20% of the pollen sum. The abundance of native canopy tree pollen declines to ~ 30% of the dryland pollen sum.

Fig. 8.5: Pages 190, 191, and 192.

A & B: Pollen stratigraphy for AL-3. The abundance of aquatic or swamp taxa is not shown as the abundance of this pollen was below 1% for the entire record. Pollen abundance is expressed as a percentage of the dryland sum (%).

C: The pollen concentration and organic content (loss-on-ignition) for AL-3.

A key is provided **in Fig. 8.5C** that provides a summary of the basic sediment types for this horizon. There are minor changes within these horizons which are shown using standard Troels Smith (1955) symbols. All the symbols and terminology used in the Troels Smith sediment description method are provided in **Appendix D**.

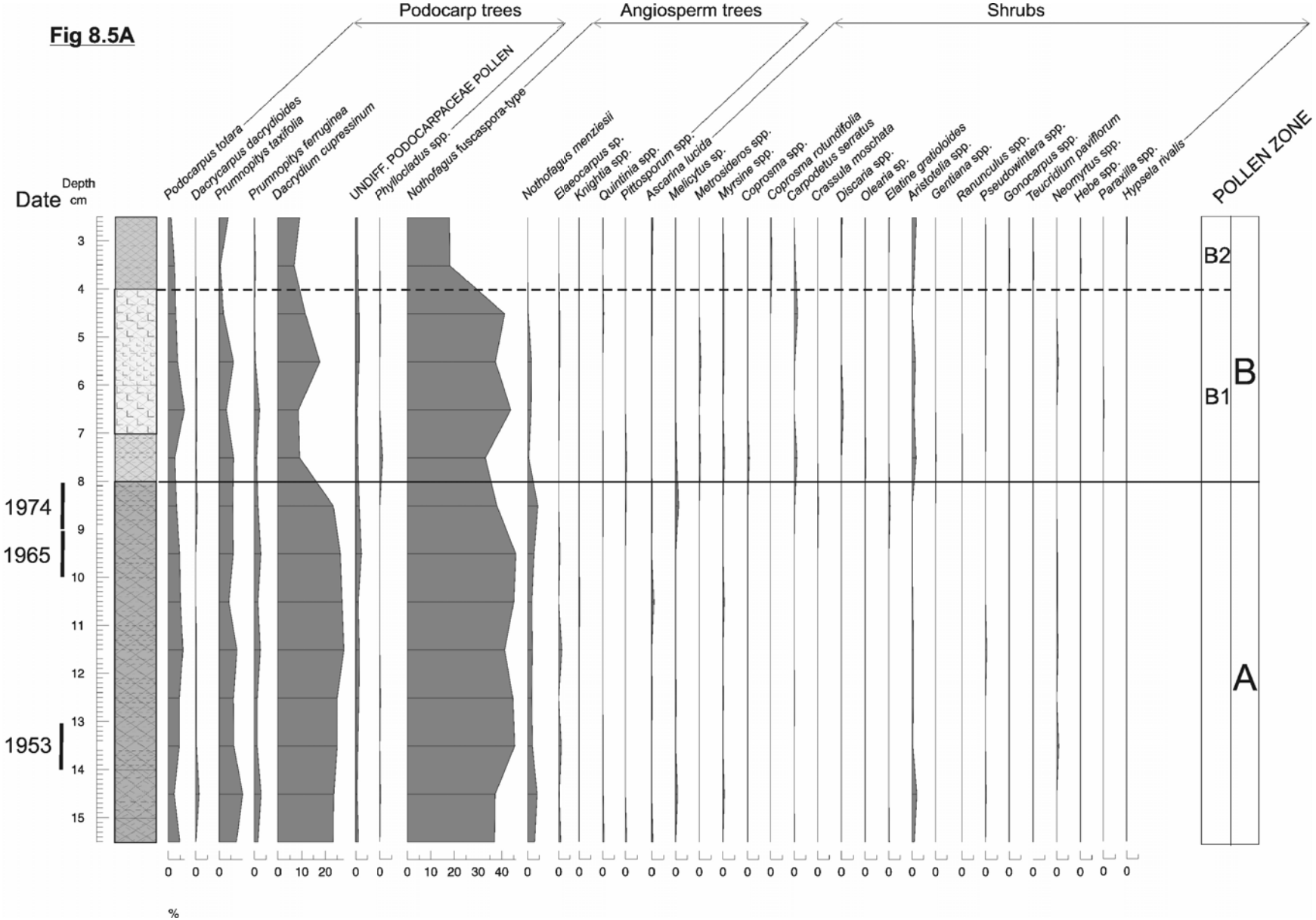


Fig 8.5A
Podocarp trees
Angiosperm trees
Shrubs
Podocarpus totara
Dacrycarpus dacrydioides
Prumnopitys taxifolia
Prumnopitys ferruginea
Dacrydium cupressinum
UNDIFF. PODOCARPACEAE POLLEN
Phyllocladus spp.
Nothofagus fuscaspora-type
Nothofagus menziesii
Elaeocarpus sp.
Knightia spp.
Quintinia spp.
Pittosporum spp.
Ascarina lucida
Melicytus sp.
Metrosideros spp.
Myrsine spp.
Coprosma spp.
Coprosma rotundifolia
Carpodetus serratus
Crassula moschata
Discaria spp.
Olearia sp.
Elatine gratioloides
Aristotelia spp.
Gentiana spp.
Ranunculus spp.
Pseudowintera spp.
Gonocarpus spp.
Teucridium paviflorum
Neomyrtus spp.
Hebe spp.
Paraxilla spp.
Hypsela rivalis
POLLEN ZONE
Date
Depth cm
1974
1965
1953
B2
B1
B
A
0 0 0 0 0 10 20 0 0 0 10 20 30 40 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0
%

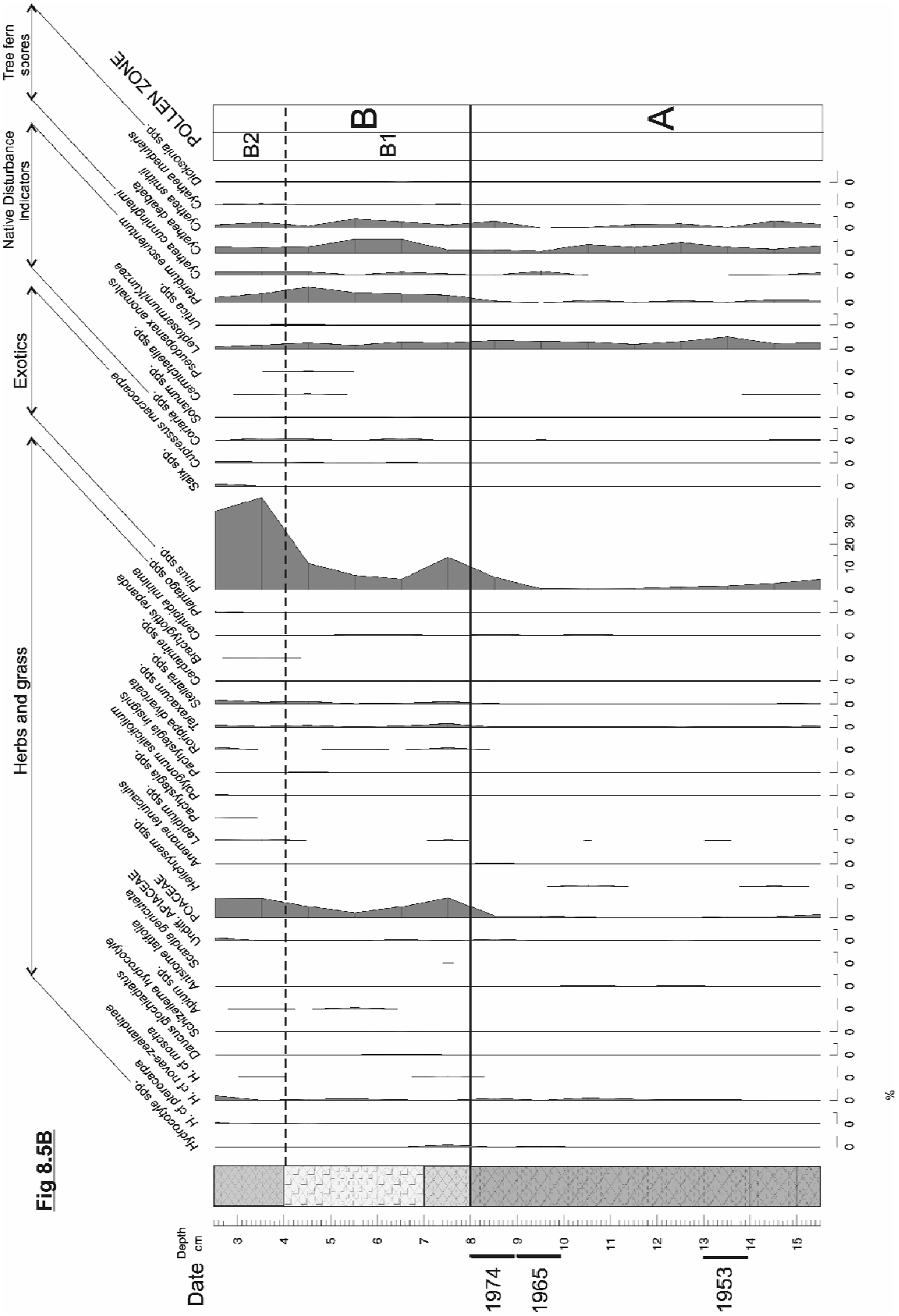
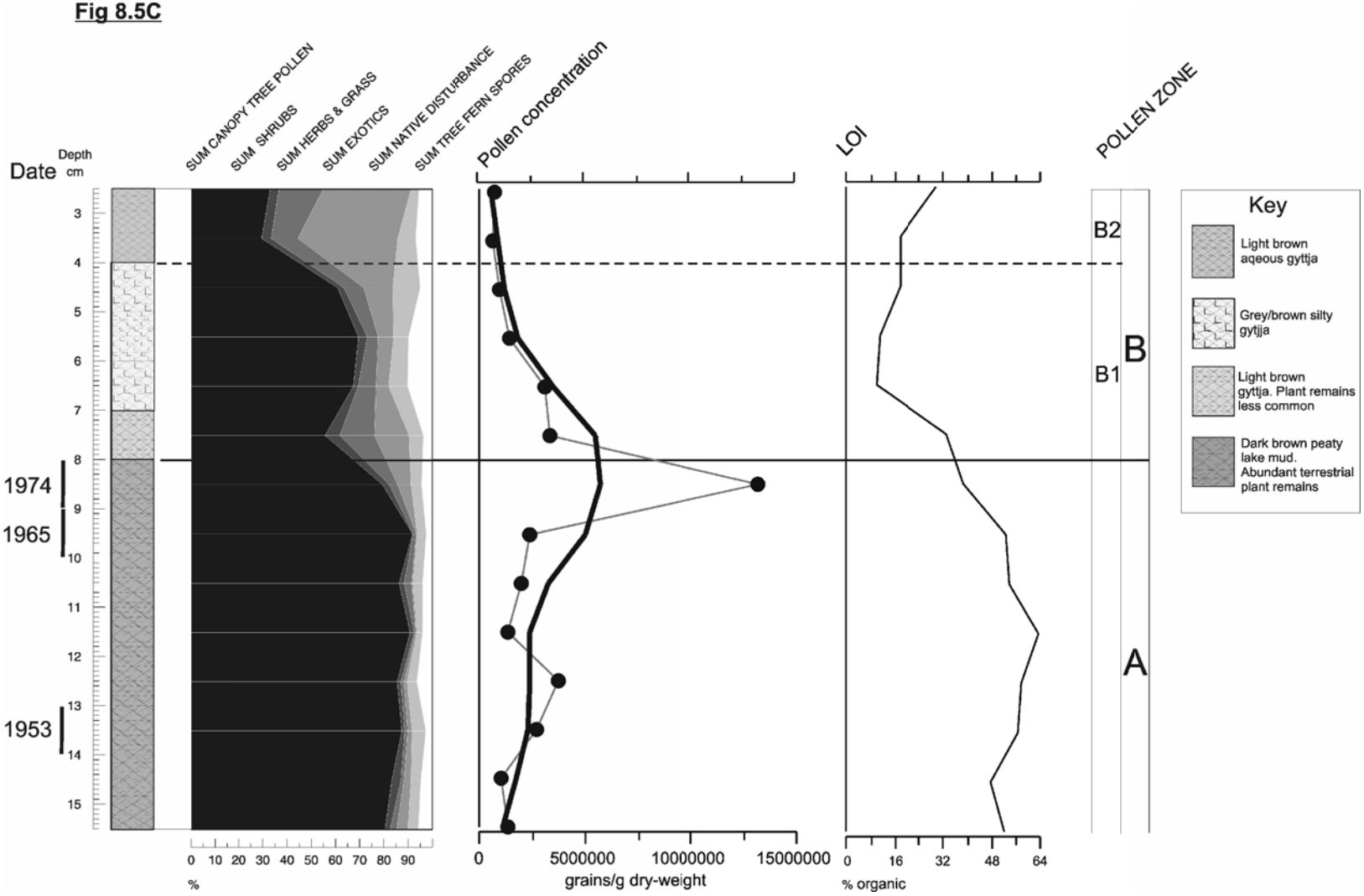


Fig 8.5B
Herbs and grass
Exotics
Native Disturbance indicators
Tree fern spores
POLLEN ZONE
Hydrocotyle spp.
H. cf. pterocarpa
H. cf. novae-zealandiae
Daucus glochidiatus
Schizeilema hydrocotyle
Apium spp.
Aristotelia fruticosa
Scandia geniculata
Undif. APIACEAE
HALORAGACEAE
Haloragis tenuicaulis
Leptospermum spp.
Peatlandia spp.
Polygonum spp.
Polygala spp.
Rorippa divaricata
Stellaria spp.
Ceratostema spp.
Brachyglottis repanda
Centipeda minima
Plantago spp.
Pinus spp.
Salix spp.
Cupressus macrocarpa
Cotula spp.
Solanum spp.
Cerastium spp.
Pseudognaphalium spp.
Leptospermum/kunzea
Urtica spp.
Pteridium esculentum
Cyathea cunninghamii
Cyathea dealbata
Cyathea smithii
Dicksonia antarctica
Dicksonia spp.
B2
B1
B
A
Depth cm
Date
1974
1965
1953
%

Fig 8.5C


SUM CANOPY TREE POLLEN
SUM SHRUBS
SUM HERBS & GRASS
SUM EXOTICS
SUM NATIVE DISTURBANCE
SUM TREE FERN SPORES
Pollen concentration
LOI
POLLEN ZONE
Date
Depth cm
1974
1965
1953
B2
B1
B
A
Key
Light brown aqeous gyttja
Grey/brown silty gytjja
Light brown gyttja. Plant remains less common
Dark brown peaty lake mud. Abundant terrestrial plant remains
0 10 20 30 40 50 60 70 80 90
%
0 5000000 10000000 15000000
grains/g dry-weight
0 16 32 48 64
% organic

8.4.3 Macrofossils

A diagram depicting the concentration of remains from various plant and animal macrofossils found in AL-3 (excluding chironomids) is provided in **Fig. 8.6.**

Plant remains

Fern sporangia were the most common macrofossils in AL-3. These were particularly common in the bottom 3cm of the core. There is a rapid decline in the abundance of fern sporangia above 12 cm. This decline continues more gradually above 11 cm, until fern sporangia were completely absent at the top of the core. Fragments of dicot leaves were also common in AL-3. Dicot leaf fragments were particularly common up until 8 cm depth, where there is a sharp decline in their abundance. Some of these fragments may belong to *Nothofagus truncata* as fragments that were identifiable as this species were also found in AL-3.

Large charcoal fragments (> 0.5 mm Ø) were present in low concentrations up unitil 8 cm in AL-3. Above this point there is a rapid increase in the concentration of charcoal fragments which peaks between 4 and 5 cm. Macroscopic charcoal particles decrease rapidly above this point and are absent at the top of the core.

Other types of plant remains, including podocarp seeds (e.g. *Prumnopityis*) and foliage from *D. cupressinum* and *Leptosermum* were also encountered in the basal 8 cm of AL-3, but were not counted.

Animal remains

Statoblasts (reproductive bodies) from the freshwater bryozoan *Plumatella* (**Fig. 8.7**) where present in low abundances below 10 cm. There is a rapid increase in the concentration of statoblasts in AL-3 above 10 cm depth. There is an abrupt reduction in the concentration of statoblasts between 4 and 6 cm. The concentration of statobalsts then increase at the top of the core to the highest values of the entire record. Head-capsules belonging to Lepidopteran larvae, and mandibles and head-capsule fragments belonging to the Trichopteran *Oecetis unicolor* were present below 7 cm in AL-3. Mites (Arachnida: Acari) were also common at the base of AL-3. The concentration of mites preserved in this core steadily declined to a constant, low concentration above 8 cm.

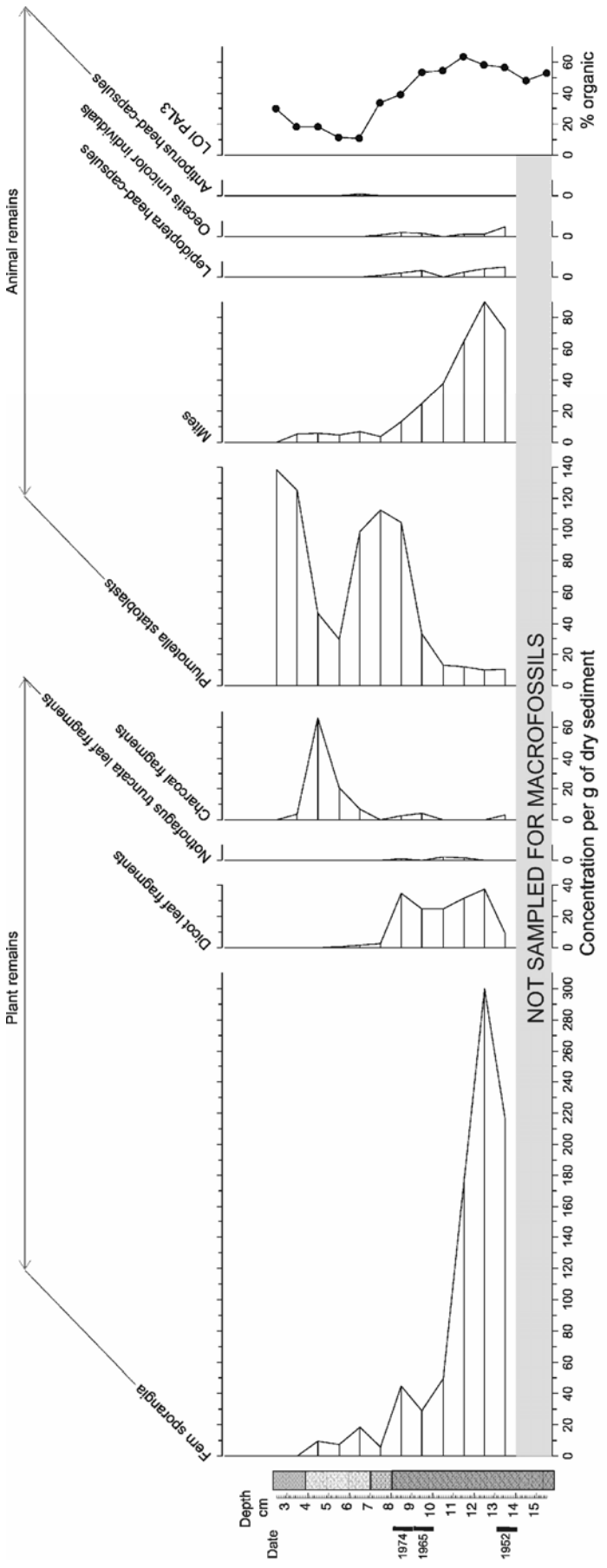


Fig. 8.6: Macrofossil stratigraphy from AL-3. The basal 2 cm were not sampled for macrofossils as the basal part of the core was mostly large wood fragments, with a minimal amount of sediment. Loss-on-ignition curve for AL-3 is also shown. Key to sediment stratigraphy is provided in **Fig. 8.5C**.

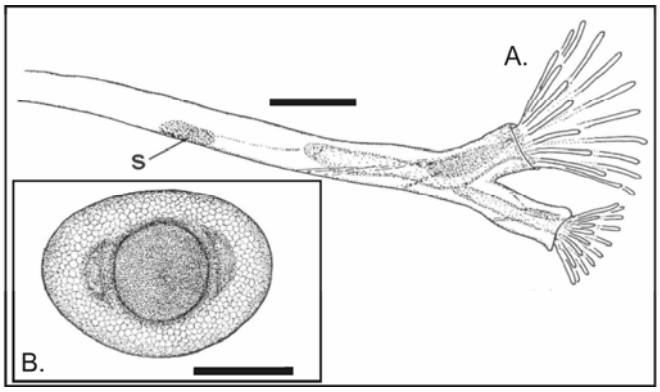


Fig. 8.7: A. Single zooid of *Fredericella* a freshwater bryozoan, showing general features. S = developing statoblast (reproductive stage). Ciliated tentacles are at the right end of the zooid.
Scale bar = 400 µm
B. Statoblast from *Plumatella* spp. showing the flat dorsal side with small finestra. Scale bar = 65 µm
Reproduced from Wood et al. (1998)

8.4.4 Chironomids

Stratigraphy

Head-capsules belonging to 21 morphotypes were enumerated from AL-3 (**Fig. 8.8**). Head-capsules belonging to *Tanytarsus funebris* and *Chironomus* spp. were the most common. The concentration of chironomid head-capsules peaked at ~ 450 head-capsules/g of dry sediment between 12 and 13 cm, then declined steadily above this point to a value of ~ 50 headcapsules/g above 6 cm. The Chironomid record was divided into 3 zones (1, 2, and 3) and 1 sub-zone (1a) based on the relative abundance of the various morphotypes (**Fig. 8.8**).

Chironomid Zone 1. Macropelopini/*Harrisius*/*Ablabesmyia* Zone (8 -14 cm). Although *Chironomus* spp., *Kiefferulus opalensis* and *Tanytarsus funebris* are common taxa in this zone (~20, 10, and 20% respectively), this zone is defined by the presence of *Harrisius* spp. and *Ablabesmyia* sp. and the abundance (10-20 %) of head-capsules belonging to the tribe Macropelopini. *Cladopelma curtivalva* is present in low abundances (<5%). The abundance of head-capsules belonging to the tribe Macropelopini decline from ~20 to 10 % at the top of this zone.

Chironomid Zone 1a. *Naonella kimihia* Zone (8 -9cm). Zone 1 was subdivided based on the appearance of *Naonella kimihia* in the top cm of this zone.

Chironomid Zone 2. *Corynocera*/*Naonella kimihia* Zone (4- 8 cm). The abundance of *N. kimihia* remains low (<5%), while there is a rapid increase, then decrease in the relative abundance of *Corynocera* sp.. There is a peak in the relative abundance of *K. opalensis* and

Chironomus spp. at the base of this Zone. *Cladopelma curtivalva* is present in low abundances (<5%) and disappears at the top of this Zone. The abundance of head-capsules belonging to the tribe Macropelopini continues to decline, while the abundance of head-capsules belonging to *Polypedilum* spp. increases towards the top of this zone.

Chironomid Zone 3. *Chironomus/ Tanytarsus/ Kiefferulus* Zone (2-3 cm). *Chironomus* spp., *Tanytarsus* funebris, *Kiefferulus opalensis* are the most common head-capsules in this zone. Head-capsules belonging to the other 18 taxa enumerated in this core are rare (< 10%) Head-capsules belonging to *N. kimihia* and *Polypedilum* spp. are at their highest abundances for the entire core, while the Macropelopini are at their lowest abundance for the entire core.

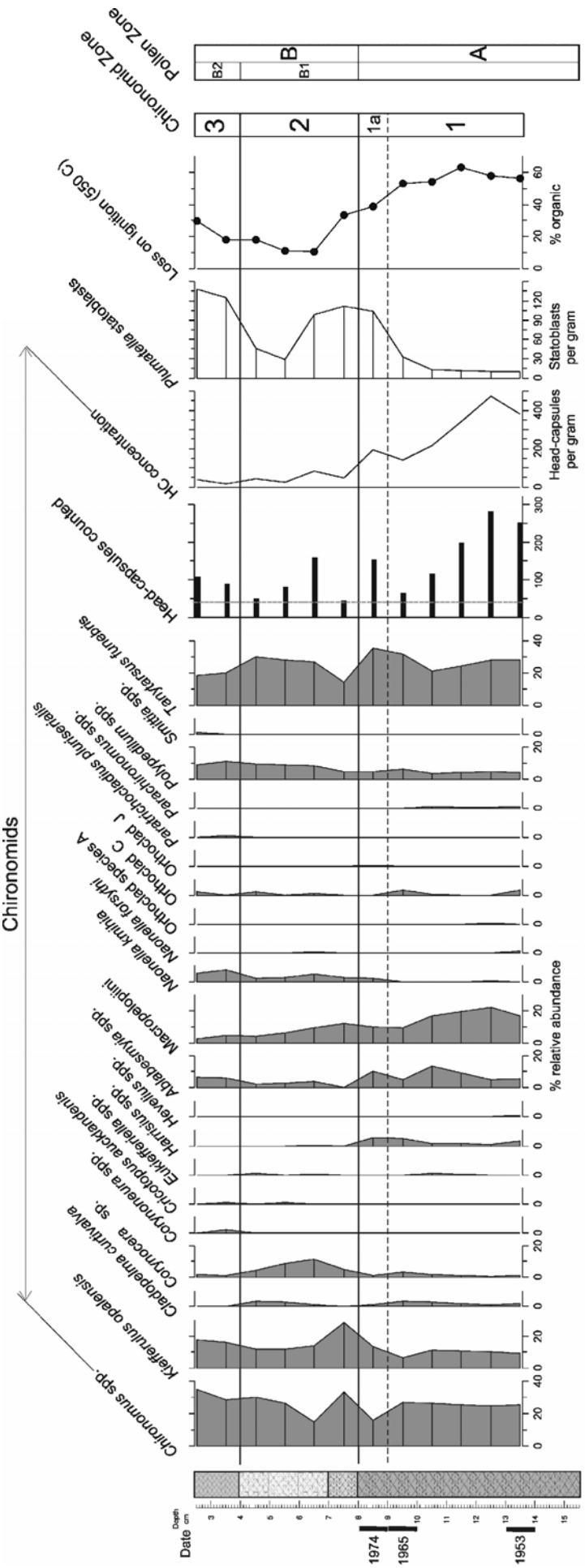


Fig. 8.8: Chironomid stratigraphy for AL-3. Relative abundance of each taxon expressed as a percentage of the total head-capsule count. At least 40 head-capsules were counted from each horizon (grey dashed line). The head-capsule concentration, the concentration of *Plumatella* statoblasts, the organic content (loss-on-ignition) and pollen zones are also shown. The key to the sediment stratigraphy is provided in **Fig. 8.5C**.

Reconstructions

Model selection

The performance statistics for the transfer functions using the 2% deletion criterion (16 taxa) and only the significant taxa (6 taxa) are depicted in **Table 8.1**. In all cases removing non-significant taxa resulted in a higher r^2_{boot} and a lower RMSEP. The PLS-based transfer-function produced the model with the highest r^2_{boot}, the lowest RMSEP for both the 2% deletion criterion taxon set and the significant taxon set. The PLS model with the 2% deletion criterion produced the highest sample specific errors (~ 0.215 Log_{10} TN/L) (**Table 8.2)** when compared to the other methods using the same taxon dataset.

The sample specific errors were slightly lower for all methods using only the significant taxa (**Table 8.2**). The PLS emerged as the preferred method for reconstructing the original trophic status of this lake because it produced the lowest average residual for the low portion of the TN gradient (**Table 8.3**).

All methods had the tendency to over-predict lower TN concentrations and under-predict higher TN concentrations (**Table 8.3**). The PLS-based models (both taxon datasets) were selected because they had the highest r^2_{boot}, lowest RMSEP, and the small average residuals at the low and high end of the TN gradient compensated for the tendency towards slightly higher sample-specific errors (**Table 8.1, 8.2 and 8.3**).

Model application

The results from the PLS-based TN reconstructions for both taxon datasets were very similar. TN concentrations were low (predicted value = -0.7 Log_{10} TN/L) and stable in AL-3 below 10 cm (**Fig. 8.9**). A fitted LOWESS smoother shows a trend of steady eutrophication above 10 cm depth with predicted TN values equivalent to eutrophic summer conditions at the top of the core. Reconstructions based on both taxon datasets predict a range between the upper end of oligotrophic and mesotrophic summer lake conditions (-0.9 - -0.5 Log_{10} TN/L). Most of the reconstructions above this point range from the lower end of mesotrophic to eutrophic conditions.

ALL TAXA

WA Bootstrapped

	#	Code	Name	R2	Boot_R2	Boot_Ave_Bias	Boot_Max_Bias	RMSE_s1	RMSE_s2	RMSEP
1	1	WA_Inv	Weighted averaging model (inverse deshrinking) for TN	**0.821001**	**0.767224**	**-0.00230402**	**0.271105**	**0.088005**	**0.193031**	**0.212146**
2	2	WA_Cla	Weighted averaging model (classical deshrinking) for TN	0.821001	0.771047	-0.0084351	0.34592	0.122087	0.203894	0.23765
3	3	WATOL_Inv	Weighted averaging model (tolerance downweighted, inverse deshrinking) for TN	0.816186	0.725322	0.0054381	0.359796	0.100588	0.210657	0.23344
4	4	WATOL_Cla	Weighted averaging model (tolerance downweighted, classical deshrinking) for TN	0.816186	0.733744	-0.000553689	0.222735	0.128913	0.213345	0.249268

WA-PLS Bootstrapped

	#	Code	Name	R2	Boot_R2	Boot_Ave_Bias	Boot_Max_Bias	RMSE_s1	RMSE_s2	RMSEP	%Change
1	1	Component 1	WAPLS Component 1 for TN	**0.821001**	**0.764931**	**-0.000373686**	**0.301545**	**0.0779637**	**0.194318**	**0.209375**	...
2	2	Component 2	WAPLS Component 2 for TN	0.88725	0.801816	-0.000773745	0.330063	0.106387	0.177861	0.207251	1.01474
3	3	Component 3	WAPLS Component 3 for TN	0.905398	0.798003	-0.00162694	0.346176	0.125275	0.181521	0.220553	-6.41867
4	4	Component 4	WAPLS Component 4 for TN	0.917788	0.789514	0.00530347	0.36362	0.147431	0.189456	0.240061	-8.84511
5	5	Component 5	WAPLS Component 5 for TN	0.925151	0.782006	0.0102872	0.379088	0.173329	0.196523	0.262039	-9.15493

PLS Bootstrapped

	#	Code	Name	R2	Boot_R2	Boot_Ave_Bias	Boot_Max_Bias	RMSE_s1	RMSE_s2	RMSEP	%Change
1	1	Component 1	PLS Component 1 for TN	0.818258	0.765539	0.00842167	0.327699	0.0926002	0.202332	0.222515	...
2	2	Component 2	PLS Component 2 for TN	**0.881144**	**0.798973**	**0.0161801**	**0.306424**	**0.0911494**	**0.180026**	**0.201786**	**9.31575**
3	3	Component 3	PLS Component 3 for TN	0.907198	0.808636	0.00992317	0.314255	0.103079	0.175255	0.203321	-0.760615
4	4	Component 4	PLS Component 4 for TN	0.919689	0.819419	0.0107325	0.326756	0.114772	0.171137	0.206059	-1.34674
5	5	Component 5	PLS Component 5 for TN	0.930339	0.824535	0.00903678	0.333068	0.127361	0.170066	0.21247	-3.11108

ONLY SIGNIFICANT TAXA

WA Bootstrapped

	#	Code	Name	R2	Boot_R2	Boot_Ave_Bias	Boot_Max_Bias	RMSE_s1	RMSE_s2	RMSEP
1	1	WA_Inv	Weighted averaging model (inverse deshrinking) for TN	**0.835317**	**0.795748**	**0.000510061**	**0.271504**	**0.0654232**	**0.180544**	**0.192032**
2	2	WA_Cla	Weighted averaging model (classical deshrinking) for TN	0.835317	0.802514	-0.00535043	0.357607	0.0836115	0.194119	0.21136
3	3	WATOL_Inv	Weighted averaging model (tolerance downweighted, inverse deshrinking) for TN	0.82453	0.746775	0.00433198	0.305666	0.0902239	0.201634	0.2209
4	4	WATOL_Cla	Weighted averaging model (tolerance downweighted, classical deshrinking) for TN	0.82453	0.757654	0.000678414	0.327598	0.109799	0.216121	0.242413

WA-PLS Bootstrapped

	#	Code	Name	R2	Boot_R2	Boot_Ave_Bias	Boot_Max_Bias	RMSE_s1	RMSE_s2	RMSEP	%Change
1	1	Component 1	WAPLS Component 1 for TN	**0.835317**	**0.788219**	**0.00199669**	**0.302695**	**0.0662723**	**0.183832**	**0.195413**	...
2	2	Component 2	WAPLS Component 2 for TN	0.872216	0.824169	0.00482339	0.372532	0.082481	0.167817	0.186991	4.30961
3	3	Component 3	WAPLS Component 3 for TN	0.880223	0.823515	0.00195728	0.385352	0.0923984	0.168839	0.192469	-2.92914
4	4	Component 4	WAPLS Component 4 for TN	0.879813	0.82217	0.000949668	0.390697	0.095383	0.169836	0.194788	-1.20487
5	5	Component 5	WAPLS Component 5 for TN	0.879823	0.822043	0.000683784	0.391461	0.0959432	0.169903	0.195121	-0.170892

PLS Bootstrapped

	#	Code	Name	R2	Boot_R2	Boot_Ave_Bias	Boot_Max_Bias	RMSE_s1	RMSE_s2	RMSEP	%Change
1	1	Component 1	PLS Component 1 for TN	0.844919	0.812213	0.00755997	0.274853	0.0746043	0.175213	0.190435	...
2	2	Component 2	PLS Component 2 for TN	**0.874645**	**0.834012**	**-0.00326325**	**0.284407**	**0.0645626**	**0.162937**	**0.175263**	7.96713
3	3	Component 3	PLS Component 3 for TN	0.895437	0.847606	-0.0020304	0.380894	0.077577	0.156127	0.174338	0.527267
4	4	Component 4	PLS Component 4 for TN	0.906729	0.853891	-0.00229339	0.405449	0.0766263	0.153068	0.171177	1.81359
5	5	Component 5	PLS Component 5 for TN	0.907492	0.85009	-0.00740944	0.412019	0.083085	0.156026	0.176769	-3.26689

Table 8.1: Performance statistics for transfer functions based on all of the taxa selected using the 2% deletion criterion (All taxa, n = 17) and a subset of these taxa that displayed a significant response to TN (n= 6)

Horizon midpoint (cm)	Bootstrapped sample sepcific error. Log_{10} TN/L					
	All taxa			Significant taxa		
	WA	WA-PLS	PLS	WA	WA-PLS	PLS
2.5	0.201641	0.202295	0.210825	0.188937	0.19455	0.194265
3.5	0.200246	0.200981	0.209345	0.185894	0.190361	0.198851
4.5	0.200294	0.201417	0.214685	0.18807	0.193454	0.197068
5.5	0.199496	0.20045	0.215135	0.185125	0.18944	0.199395
6.5	0.200526	0.201872	0.214166	0.185709	0.191896	0.206681
7.5	0.200898	0.202622	0.214368	0.186119	0.190389	0.201871
8.5	0.202888	0.203258	0.214527	0.186118	0.190518	0.199775
9.5	0.20196	0.202786	0.220145	0.186225	0.190802	0.200914
10.5	0.204013	0.203846	0.219525	0.186485	0.190419	0.205383
11.5	0.202848	0.203178	0.219446	0.186463	0.190408	0.208619
12.5	0.202696	0.203598	0.220655	0.186447	0.190401	0.21175
13.5	0.204288	0.205966	0.221819	0.1867	0.192973	0.211877
Average	**0.201816**	**0.202689**	**0.21622**	**0.186524**	**0.191301**	**0.203037**

Table 8.2: Sample specific errors for the samples in AL-3 using the transfer functions based on different methods Ans different taxon deletion criteria.

Observed TN	Residual (predicted - observed values)					
	All taxa			Significant taxa		
	WA_Inv_X	WAPLS_C1_X	PLS_C2_X	WA_Inv_X	WAPLS_C1_X	PLS_C2_X
-0.977	0.295	0.297	0.177	0.259	0.242	0.121
-0.939	0.352	0.356	0.318	0.298	0.303	0.297
-0.843	0.357	0.343	0.247	0.255	0.253	0.197
-0.841	0.211	0.207	0.020	0.164	0.164	0.034
-0.826	0.140	0.134	0.231	0.117	0.127	0.149
-0.740	0.126	0.135	0.117	0.124	0.131	0.121
-0.709	0.136	0.119	0.022	-0.016	0.001	0.016
-0.646	0.126	0.128	0.192	0.084	0.090	0.135
-0.620	0.166	0.183	0.074	0.169	0.164	0.057
-0.550	-0.035	-0.030	-0.201	-0.056	-0.055	-0.152
-0.510	-0.080	-0.067	-0.098	-0.108	-0.095	-0.040
-0.487	-0.009	-0.036	0.032	0.022	0.031	0.046
-0.483	0.076	0.077	0.066	-0.015	-0.023	0.037
-0.469	0.026	0.033	0.013	0.025	0.021	0.051
-0.398	-0.221	-0.196	-0.284	-0.158	-0.156	-0.214
-0.393	-0.107	-0.111	-0.094	-0.079	-0.084	-0.050
Average	**0.098**	**0.098**	**0.052**	**0.068**	**0.070**	**0.050**
-0.388	-0.185	-0.166	-0.159	-0.319	-0.324	-0.248
-0.346	-0.014	-0.004	0.001	-0.084	-0.092	-0.024
-0.326	-0.106	-0.109	-0.231	-0.183	-0.191	-0.195
-0.294	-0.104	-0.091	-0.209	-0.082	-0.082	-0.164
-0.234	-0.319	-0.324	-0.276	-0.232	-0.246	-0.168
-0.229	-0.103	-0.109	0.039	-0.065	-0.065	0.118
-0.151	-0.301	-0.285	-0.225	-0.253	-0.255	-0.175
-0.149	0.173	0.189	0.279	0.434	0.446	0.389
-0.139	-0.269	-0.262	-0.149	-0.063	-0.071	-0.112
-0.057	-0.135	-0.193	0.022	-0.174	-0.165	0.141
0.120	-0.231	-0.240	-0.258	-0.007	0.004	-0.190
0.190	0.010	-0.032	0.116	0.185	0.168	0.061
0.367	-0.003	-0.003	-0.079	-0.132	-0.151	-0.020
0.433	0.260	0.259	0.023	0.067	0.071	0.115
0.594	-0.270	-0.302	-0.306	-0.272	-0.303	-0.284
Average	**-0.107**	**-0.111**	**-0.094**	**-0.079**	**-0.084**	**-0.050**

Table 8.3: The residuals for each transfer-function based on a different method (unimodal vs linear) and a different taxon deletion criterion. The average values for the lower and upper section of the TN gradient are provided for each case.

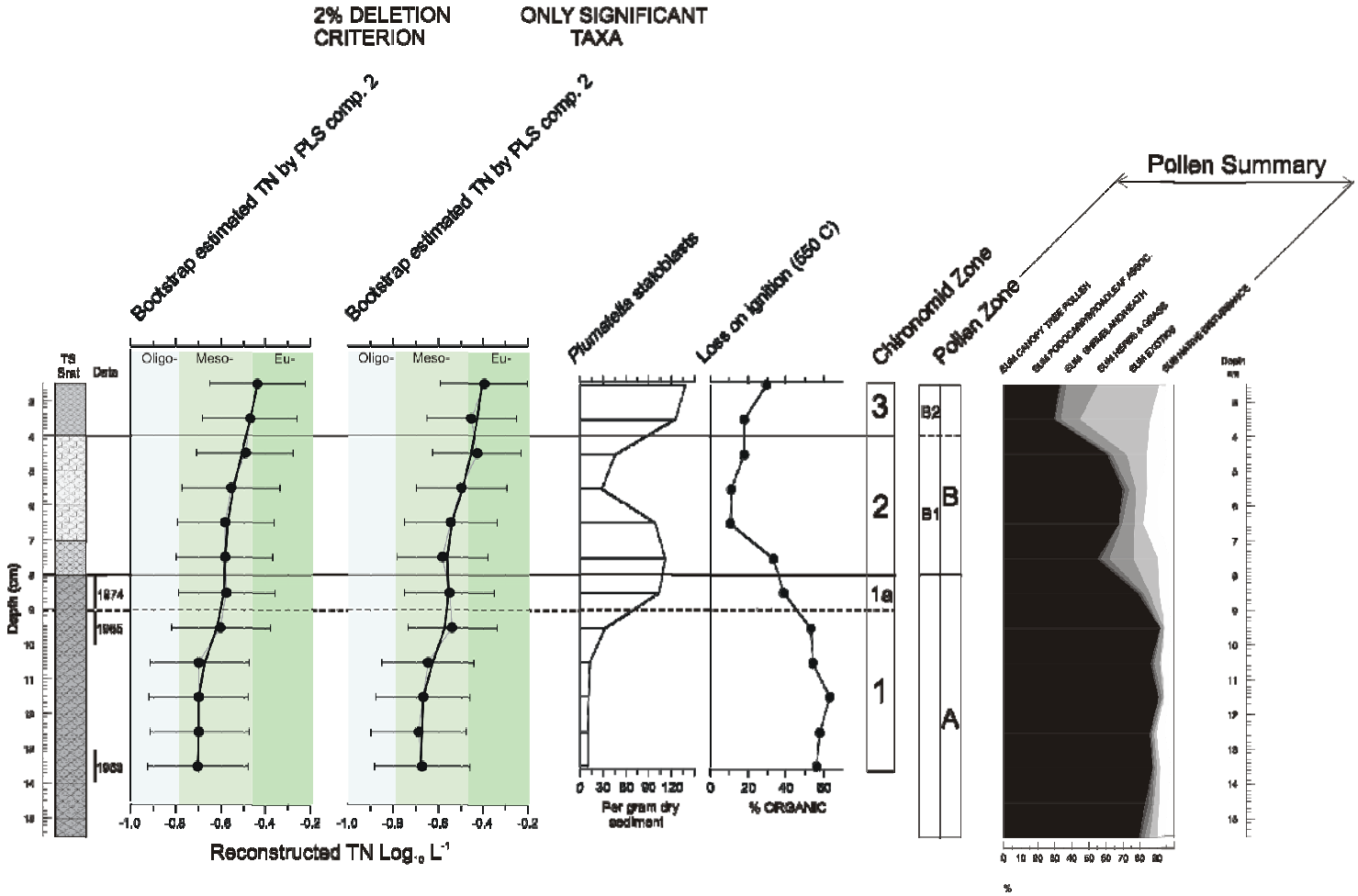


Fig. 8.9: Chironomid-based TN reconstructions for all of the taxa present in abundances >2% in at least 2 lakes (2% deletion criterion, n=17) and only those with a significant response to TN (n= 6). Trophic levels based on definitions by Burns et al. (2000).
TN reconstructions are compared with the concentration of *Plumatella* statoblasts, the organic content (LOI) and a summary of the pollen diagram. The onset of eutrophication in the chironomid record coincides with the proliferation of *Plumatella*.
Key for the sedimentary stratigraphy is depicted in **Fig. 8.5C**.

8.5 DISCUSSION

8.5.1 Chronology and correlation between cores

It is not possible to use the ^{210}Pb data (**Fig. 8.4**) to provide reliable age constraints for this core. AL-1 is too short to extend into the zone where all unsupported ^{210}Pb is decayed. It also appears that the deposition of un-supported ^{210}Pb into the lake sediments has been not been constant. If the deposition of un-supported^{210}Pb was constant, I would expect to see a logarithmic decrease in the activity of this nuclide with respect to depth (Whitehead et al., 1998). A major decrease in the activity of ^{210}Pb between 2.5 and 4.5 cm (**Fig. 8.4**) appears to correspond to an increase in allogenic sedimentation. The peak in ^{210}Pb activity at 7.5 cm depth appears to correspond to a reduction in allogenic sedimentation.

The ^{210}Pb peak corresponds to a peak in the concentration of pollen between 8 and 9 cm depth in AL-3 which I also interpret as a reduction in allogenic sedimentation. This data is also used to support the correlation between AL-1 and AL-3. The sediment description suggests an offset of 1cm between AL-1 and AL-3 (**Fig. 8.4**). The peak in pollen concentration occurs in AL-3 between 8 and 9 cm, while the peak in unsupported ^{210}Pb activity occurs between 7 and 8 cm.

Even though the ^{210}Pb data does not provide any firm ages, it does provide an indication of the relative sedimentation rates throughout the core, with a phase of reduced sedimentation rate between 6 and 9 cm and a period of increased sedimentation rate between 3 and 6 cm. The suggestion of increased allogenic sedimentation between 3 and 6 cm is also supported by the drop in sediment organic content (loss-on-ignition) which is more pronounced above 6cm depth in Al-1 and occurs in the correlative horizon in AL-3 above 8cm (**Fig. 8.4**)

The ^{137}Cs and ^{239}Pu data does provide a constraint on the chronology of AL-1 and by inference AL-3. The lack of ^{239}Pu activity in the basal sample of AL-1 (**Fig 8.4**) indicates that the base of the core must pre-date the increase in ^{137}Cs in New Zealand in 1953. The presence of *Pinus* spp. in the basal sample of AL-3 (**Fig 8.5**) provides an upper age limit. Because *Pinus* spp. is an introduced tree the basal sediments must post-date European settlement (1840).

There is a peak in the activity of ^{137}Cs and ^{239}Pu between 8 and 9 cm in AL-1 (**Fig 8.4**). The peak concentration of ^{137}Cs in New Zealand rain-water occurred in 1965 (Whitehead et al., 1998). I therefore assign an age of 1965 to the horizon between 8 and 9 cm.

Determination of the horizon corresponding to the end of significant (USA, USSR, and France) atmospheric testing (1974 AD) is more problematic because there is a low amount of activity for both ^{137}Cs and ^{239}Pu almost to the top of the samples section (**Fig 8.4**). I nominate the horizon between 7 and 8 cm as the most likely candidate for the end of this period due to the

rapid decline in activity for both ^{137}Cs and ^{239}Pu at this point in the core. This selection also makes sense in light of the pollen and macrofossil record. Evidence for local deforestation suggests an initiation between 8 and 9 cm in AL-3 due to the decline in dicot leaf fragments (**Fig. 8.6**) and pollen from native canopy trees, particularly *Dacrydium cupressinum* (**Fig. 8.5**).

There was a continued low concentration of atmospheric ^{137}Cs in New Zealand until 1993 due to stratospheric transfer from the Chinese nuclear weapons tests (1976-1980) (Matthews, 1995). The increase in allogenic sedimentation above 8 cm could amplify the effect of the low atmospheric ^{137}Cs concentrations. Most ^{137}Cs (and rare earths) is absorbed on muscovite (Francis and Brinkley, 1976) an increase in allogenic sediment input into the lake could increase the proportion of muscovite in the lake sediments. The increase in detrital material is supported by the loss-on-ignition data (**Fig. 8.5C**). Whitehead et al. (1998) also observed unusually high ^{137}Cs activity in the upper-most section of a core from Lake Pukaki, in the South Island, New Zealand and attributed this to an increase in the input of muscovite into the lake due to local earth-moving associated with hydroelectric projects.

8.5.2 The record of vegetation change in Alexander Lake

As I mentioned in the previous section, there is good evidence that the peak in ^{137}Cs and ^{239}Pu activity between 8 and 9 cm (**Fig. 8.4**) marks the 1965 peak in radioactive fallout from atmospheric nuclear testing. This means that the reduction in the relative abundance of native canopy tree pollen (e.g. *Dacrydium cupressinum*) from ca 80 to 60% between 7 and 9 cm in AL-3 (**Fig. 8.5**) is a signal of the clearance of the lower reaches of the Lake Alexander catchment ca 1970 (P. Alexander pers comm..). The inference that this is a local forest clearance is supported by the reduction in dicot leaf fragments between 7 and 8 cm (**Fig. 8.6**). The pollen from *D. cupressinum* and *Nothofagus menziesii* appears to provide the most accurate signal for local forest clearance and corresponds best to the plant macrofossil record. The abundance of the pollen from these taxa declines sharply in synchrony with the dicot leaf fragments ca 1974 (**Fig. 8.5A & B** and **8.6**).

This is probably due to the fact that the pollen from these taxa tends to be proportionately or under-represented in pollen assemblages when compared to the relative area of vegetation cover (Pocknall, 1978; Macphail and McQueen, 1983). Continued low abundances of pollen from the native conifers to the top of the core is probably sourced from the surviving forest fragment on the south-western side of the lake (**Fig. 8.1**). Pollen re-worked from the soil immediately surrounding the lake may also contribute to the continued presence of pollen from native canopy trees above 8 cm, particularly where there is a pulse of allogenic sedimentation between 4 and 7

cm (**Fig. 8.5**). There is a slight increase in the proportion of tree-fern spores between 5 and 7 cm depth in AL-3 without a corresponding increase in the concentration of fern sporangia (**Fig. 8.5** and **8.6**). Dunbar et al. (1997) and Wilmshurst & McGlone (2005) have shown that the relative abundance of fern spores is greater in allogenic sediment. A pollen assemblage dominated by pollen re-worked from the soil immediately surrounding the lake may also explain why the proportion of *Pinus* spp. remains low until authigenic sedimentation resumes above 4 cm.

The pulse of allogenic sedimentation between 4 and 7 cm could correspond to a period of stabilization immediately after deforestation in the lower Alexander Lake catchment. A pulse of inorganic sedimentation could also correspond to a major storm that caused severe flooding in the Takaka Valley in 1983. The 1983 storm resulted in a rainfall in excess of 600 mm in a 48 hour period (Clark 1983). I believe that the pulse of inorganic sedimentation is most likely to be due to the 1983 storm as the ^{210}Pb activity and pollen concentration data actually suggest that there was a period of reduced sedimentation directly after deforestation (**Fig. 8.4**). Prior to local deforestation the dominant sediment input into Alexander Lake was allocthonous organic material from the surrounding forest, i.e. leaves, twigs etc. (forest litter). Even though a patch of the surrounding forest remains on the south-western side (**Fig. 8.1**) enough of the surrounding forest was removed ca 1970 to severely reduce the input of forest litter.

8.5.3 Evidence for the impact of human activity on Alexander Lake

Evidence for clearance of the vegetation in the immediate vicinity of Alexander Lake first occurs in the AL-3 record between 8 and 9 cm as a decline in the abundance of native canopy tree pollen (**Fig. 8.5**) and the abrupt reduction in concentration of dicot leaf fragments (**Fig. 8.6**). Chironomid-based TN inferences (**Fig. 8.9**) indicate the possibility that eutrophication started in the record 1 cm below this. A loess smoother fitted to the chironomid-based TN reconstructions (**Fig. 8.9**) indicates a possible increase in the trophic status of Alexander Lake about 1965. However, the concentration of *Plumatella* statoblasts does not drastically increase until 1974 and the remains if *Oecetis unicolor* are present in low numbers until between 7 and 8 cm (**Fig 8.6**).

Freshwater bryozoans such as *Plumatella* feed on suspended organic particles in the water which they capture with a whorl of ciliated tentacles (**Fig. 8.7**). Wood et al. (1998) reported the greatest biomass of freshwater bryozoans in New Zealand waters where the water was "somewhat eutrophic, appearing turbid or coloured" (pp. 646). *O. unicolor* is absent from highly productive lakes, but can tolerate mesotrophic conditions (Stark 1981; Timms 1982 and 1983). The peak in *Plumatella* statoblasts accompanied by the disappearance of *O. unicolor* suggests a

switch to higher productivity with a greater concentration of suspended organic particles after the clearance of the vegetation around the lake ca 1974.

Even though the quantitative TN reconstructions infer a possible increase starting between 9 and 10cm depth, the major switch in the chironomid fauna does not occur until 8 cm (Zone 1/2 transition. **Fig. 8.8**), which is in keeping with the switch to a more productive system that is suggested by *Plumatella* and *O. unicolor*. The main changes to occur at the chironomid Zone 1/2 transition are the almost complete disappearance of *Ablabesmyia* spp. and *Harrisius* spp. and an increase in the abundance of *Naonella kimihia, Corynocera* sp. and *Polypedilum* spp. The trophic tolerance of *Harrisius* spp. was not constrained in the modern training set as it was a rare taxon. The disappearance of this taxa following local deforestation is probably due to a reduction in the input of woody debris into the lake. Anderson (1982) reported that *Harrisius* is truly xylophagous (feeds on wood) based on a study of the gut contents of this genus in New Zealand.

Ablabesmyia was observed to be more common in the modern training set (**Chapter 5**) in lakes with a summer trophic level ranging from oligotrophic to mesotrophic, while *N. kimihia* and *Polypedilum* spp. were more common in more productive (mesotrophic-eutrophic lakes). Previous studies from elsewhere in the world have shown increased abundances of *Polypedilum* in response to moderate increases in trophic status (e.g. Warwick, 1975; Brodin, 1982; Hall et al., 1999). It has been observed in a previous study by Boubee (1983) that *N. kimihia* is typically associated with macrophytes. A moderate increase in trophic status after 1974 could have led to the proliferation of macrophytes in the narrow littoral zone of this lake. It is interesting to note that the remains of macrophytes, including charophyte oospores, were absent in AL-3.

Schakau (1993) also observed an increase in the abundance of *N. kimihia* (which she called Orthocladiinae sp. IX) following a signal for Polynesian deforestation in the pollen record. Schakau (1993) inferred the increase in the abundance of *N. kimihia* to be indicative of a rise in lake productivity as well as increased input of allochthonous material caused by frequent fires. The increase in the abundance of *Corynocera* sp. in chironomid Zone 2 in Alexander Lake is more difficult to explain. This taxon has typically been associated with shallow clear-water lakes in New Zealand in previous studies (Boubee, 1983; Schakau, 1993). Both the chironomid-based reconstructions and the abundance of *Plumatella* statoblasts (**Fig. 8.9**) indicate productive turbid conditions in the lake at this time, at least during the summer. *Corynocera* sp. head-capsules were also abundant (~ 18 %) in Lake Emma, which was also turbid, with a secchi depth of 0.7m and a chlorophyll *a* concentration of 2.1 µg/L (**Table B1 and B2, Appendix B**). Live *Corynocera* sp. larvae were also found in a benthic grab sample taken from the deepest point in Lake Emma (~2 m).

This data suggests that *Corynocera* sp. in New Zealand is not strictly an oligotrophic indicator taxon. It is possible that more than one species occurs in New Zealand as *Corynocera* sp. was found in lowland eutrophic lakes and high altitude oligotrophic lakes in the modern training set (**Chapter 5**). Another possibility is that *Corynocera* sp. is also limited by some other environmental factor. Boubee (1983) reports *Corynocera* sp. in New Zealand lakes with a distinct substrate consisting of a flocculant organic layer with a very high concentration of diatom algae and decaying reeds. Boubee (1983) also found the gut contents of *Corynocera* sp. larvae comprised diatom/algal detritus and mineral grains. The increase in the abundance of *Corynocera* sp. could therefore be due to an increased production of planktonic algae, which is supported by the chironomid-inferred TN concentration and the abundance of *Plumatella* statoblasts. A reduction in the abundance of *Corynocera* sp. near the top of the core could be the result of more advanced eutrophication, resulting in a reduction in the availability of dissolved oxygen. Both *Corynocera* sp. and the Macropelopini are dependent on moderate levels of dissolved oxygen (Boubee, 1983).

It is also interesting to note that most of the chironomid taxa seem to be relatively un-affected by the pulse of allogenic sedimentation between 4 and 7 cm. *N. kimihia* and *Ablabesmyia* are possible exceptions. *Ablabesmyia* appears to be less abundant in chironomid Zone 2, while there appears to be a slight increase in the abundance of *N. kimihia* above 4 cm in AL-3. There is a reduction in the concentration of *Plumatella* statoblasts that is co-incident with the low organic content and rapid sedimentation between 4 and 6 cm (**Fig. 8.6**). It is not clear whether this is a drop in production or merely a dilution of the *Plumatella* statoblasts due to an increase allogenic sedimentation. Francis (1997) reported a rapid decrease in *Plumatella* populations recorded following local deforestation in a short sediment core from Douglas Lake, Michigan. Francis (1997) attributed the decline in *Plumatella* populations to increased sediment loads interfering with the feeding of these animals.

8.5.4 Reliability of the chironomid-based TN reconstructions

One possible source of error for the TN reconstruction based on the 2% deletion taxon dataset is the presence of two taxa (*Chironomus* spp. and *Corynocera*) that have a response that does not show a significant fit to any of the tested response models in **Chapter 6**. It is interesting to note that the removal of these taxa from the inference model does not make a large difference to the TN reconstructions (**Fig. 8.9**) but does result in a reduction in the sample specific error (**Fig. 8.9**, **Table 8.2**). Another possible problem is the presence of a common taxon (*Kiefferulus opalensis*) that only occurred in one lake (Lake Rotorua S) in the modern training set. The abundance of *K.*

opalensis remains relatively constant for the entire record, except for a peak between 7 and 8 cm. Lake Rotorua S was a shallow (~ 2m) hypertrophic lake (TN = 0.8 Log_{10} mg/L). It therefore seems that trophic status is not a limiting factor for *K. opalensis*. Evidence presented by Forsyth (1975) and Boubee (1983) suggests that *K. opalensis* may prefer reeds or submerged branches (particularly *Leptospermum*) as a substrate. *Leptospermum scoparium* is still common around the margins of the lake, and *Leptosermum*/*Kunzea* pollen is present consistently throughout the record.

The other possible problem is the large sample specific error compared to the amount of inferred change in the TN concentration (**Fig. 8.9**). Despite the size of sample specific errors, the fitting of a LOESS smoother produces a trend that is consistent with the historical record of eutrophication, and closely matches the information provided by the other proxies. The real difficulty lies in defining the trophic status of this lake at any point in time, which would be desired if we wanted to establish a baseline condition for this lake.

The chironomid TN reconstructions suggest a range from oligotrophic to mesotrophic as the trophic state of this lake about 1952 to 1960 (10-14 cm). This excludes the possibility that the lake was eutrophic prior to forest clearance, which is supported by the historical observations. Examining a plot of predicted vs observed TN concentrations (**Fig. 8.10**) might provide further constraint for the baseline TN estimates.

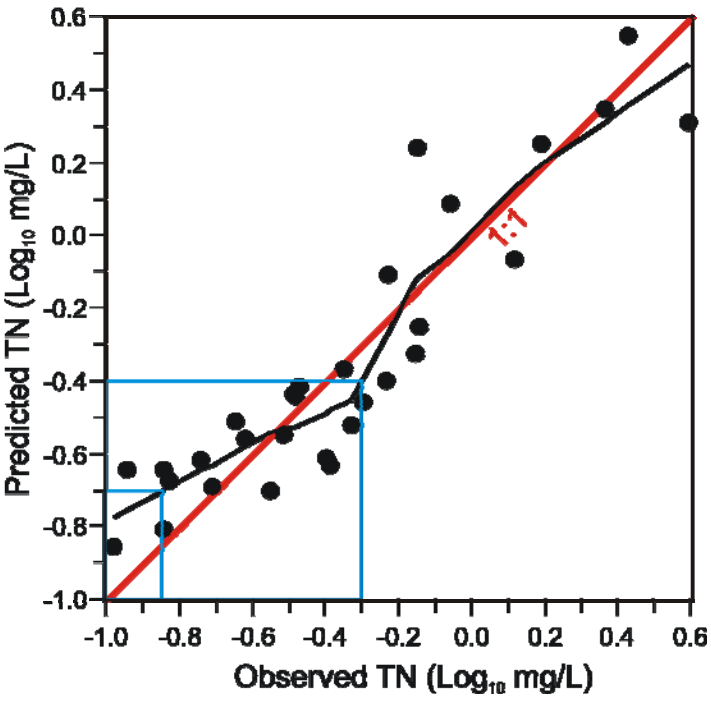


Fig. 8.10: Predicted vs observed TN values for the PLS model with 2 components with only the significant taxa (n =6). The lower and upper predicted values from AL-3 are shown as a horizontal blue line. The lower inferred value (-0.7 Log_{10} TN mg/L) most likely over-estimates the actual TN concentration by ~ 1.25 Log_{10} TN mg/L. The upper inferred values (-0.4 Log_{10} TN mg/L) most likely under-estimates the actual TN concentration by 0.1 Log_{10} TN mg/L.

The lower inferred value (-0.7 Log_{10} TN mg/L) most likely over-estimates the actual TN concentration by ~ 1.25 Log_{10} TN mg/L. This means that the original trophic status of this lake is most likely oligotrophic, or ~ 0.85 Log_{10} TN mg/L (0.14 mg/L TN). Conversely, the upper TN prediction most likely under-estimates the actual TN concentration by 0.1 Log_{10} TN mg/L. The adjusted upper TN value is therefore most likely -0.3 Log_{10} TN mg/L (0.5 mg/L). This represents an increase in TN concentration of approximately 0.36 mg/L.

8.5.5 The causes of eutrophication in Alexander Lake

It is clear from the paleolimnological record and actual observations that serious eutrophication in Alexander Lake did not occur until a remant patch of regenerating native forest was cleared from the immediate vicinity of the lake. A longer record would be required to verify whether the oligotrophic status indicated by the chironomids is the pre-disturbance state in this lake.

The lack of an inflowing stream into the lake probably limited the inflow of nutrients into the lake from the surrounding land although dissolved nutrients (phosphates and nitrates) may have entered the lake from the adjacent land via subcutaneous flow through the terrace gravels or fissures in the underlying marble.

The existence of native forest around the lake, and the resulting input of plant matter could also have acted as a "buffer" limiting phytoplankton primary production. Coloured humic substances restrict phytoplankton primary production by the absorption of light. The euphotic zone in humic lakes with dissolved organic carbon (DOC) concentrations of 10-15 mg/L is only 1-2 m, while it extends to depths of greater than 10 m in Clearwater lakes (Jones, 1992). Apart from during storm events, there still seems to be a limited overland flow of water from the surrounding land into the Alexander Lake. It could be that the input of dissolved nutrients was high enough to encourage high algal production prior to local deforestation. The removal of the adjacent stand of native scrub could have lowered the input of DOC, increasing the depth of the photic zone, consequently encouraging algal growth.

One other possible trigger for eutrophication after forest clearance is the arrival of large numbers of native Paradise Shelducks (*Tadorna variegata*) after the surrounding scrub was cleared (P. Alexander pers. comm.). The Paradise Shelduck is one of the few New Zealand endemic species that has benefited from major anthropogenic modification of the landscape. As land was cleared for farming in New Zealand, the paradise shelducks' habitat range expanded and their distribution increased (Williams, 1971).

Since Alexander Lake is small, it is possible that the input of nutrients from these birds (termed "guanotrophy") could be an important source of nutrients. Previous studies have shown that waterfowl faeces contain a low ratio of N to P (Mitchell and Wass 1995) which may also favour high pelagic productivity in lakes where the faecal component of the nutrient load is large. It may be possible to assess whether the Paradise duck is a major source nutrients in Alexander Lake by examining the isotopic composition of N and P in Paradise Shelduck faeces and performing the same analysis of the N and P in the lake sediments (Richard Holdaway pers. comm.).

8.6 CONCLUSIONS

The chironomid-based total nitrogen (TN) reconstructions show a shift from oligotrophic to mesotrophic conditions in Alexander Lake that coincides with the removal of a remnant forest patch in the vicinity of this lake. The chironomid record implies continued eutrophication after forest clearance with a decreasing probability of mesotrophic conditions up-section. The occurrence of serious eutrophication after deforestation is also supported by an increase in *Plumatella* (freshwater bryozoan) stomatoblasts and the disappearance of the caddisfly larva *Oecetics unicolor* from the record after 1974. TN reconsructions match actual observations of lake conditions which suggest that serious eutrophication of Alexander Lake occurred after local forest clearance ca. 1970.

Transport of dissolved nutrients from the surrounding land through subcutaneous flow may have caused a slight increase in production prior to local forest clearance, but eutrophication was limited either by the lack of drainage from the adjacent land or the limiting effect of high dissolved organic carbon (DOC) on planktonic algal production. Forest clearance would have reduced the input of allochthonous organic material into the lake thus reducing the concentration of DOC and increasing the depth of the photic zone. A reduction in DOC with the possible effects of nutrients derived from the arrival of large numbers of the Paradise Shelduck (*Tadorna variegata)* are possible triggers for the switch to a turbid highly productive condition in Lake Alexander.

Several common taxa in the Alexander Lake record were either rare in the modern training set or did not show a significant relationship to TN when tested using various response models. In the case of *Harrisius* sp. and *Kiefferulus opalensis* it appears that the input of woody detritus and the availability of *Leptospermum* branches as a substrate (respectively) were important controlling factors. The *Chironomus* spp. morphotype was a common component of the

chironomid fauna in Alexander Lake. Further work is required to enable the separation of *Chironomus* spp. into different species based on head-capsule morphology so we can understand the environmental controls on the individual taxa.

CHAPTER 9 SYNTHESIS

This chapter reviews the aims of this thesis and summarises the major research outcomes, identifies the problems and describes possible directions for future research. My discussion of future research potentials will mainly focus on the refinement of New Zealand chironomid-based transfer functions for temperature and lake production. However I will also mention some other possibilities that have not yet been explored in New Zealand, including other biological and geochemical proxies.

The outcomes of this thesis clearly demonstrate that New Zealand chironomids can be used as quantitative proxies for temperature and lake trophic status (total nitrogen (TN)). The transfer functions that have been developed are robust and appear to be producing reconstructions that are in agreement with other proxies (in the case of the temperature model) and historical observations of lake conditions (for the total nitrogen model). It has also become evident through the course of this research that there are many other useful indicator taxa (caddis-fly larval remains, freshwater bryozoan stomatoblasts) that are commonly preserved and abundant in New Zealand lake records. At this stage these taxa have provided invaluable corroborating lines of evidence that have served to constrain or re-enforce the story provided by the chironomids.

9.1 Review of thesis aims

The two main aims for this thesis were to:

1. Develop quantitative inference models (transfer-functions) for environmental variables based on the abundance of chironomid head-capsules preserved in modern lake sediments

2. Apply the resulting robust transfer-functions to dated lake records.

The application of the transfer-functions was to serve as a test for these inference models, by comparing the results with other proxies and actual observations of changes in lake condition (for the TN model). A trial core was also taken from Lake Forsyth (**Chapter 3**) prior to the development of the transfer-functions to investigate the potential for the use of chironomids in brackish lakes and coastal lagoons. This record highlighted some potential difficulties with using New Zealand chironomids as proxies for nutrients or lake production in these settings. This meant that this thesis focused on developing chironomids as a proxy for the trophic status of New Zealand fresh-water lakes.

The application of the temperature transfer function to the Lyndon Stream record (**Chapter 7**) was also intended to provide further insight into the climate conditions in New Zealand between ca. 26.6 and 24.5 ka BP (MIS 3/2 transition). Previous research has cited evidence from macrofossils (Soons and Burrows, 1978) and beetles (Marra et al., 2006) from this site for a warming or interstadial in New Zealand at this time. The temperature inferences from these previous studies were based on a single basal sample. The chironomid-based temperature reconstructions spanned the entire exposed section of lake silts in Lyndon Stream and served as corroborating evidence for the beetle and macrofossil based reconstructions. The maximum amount of cooling for this time period was the key question for the Lyndon stream site. The mild cooling inferred from the previous temperature estimates (Soons and Burrows, 1978; Marra et al., 2006) is insufficient by itself to explain the lack of canopy tree pollen in the same sample from Lyndon Stream examined by Soons and Burrows (1978) and pollen records from elsewhere in New Zealand (Moar, 1980; Moar and Suggate, 1996).

Since Boubee (1983) and Shakau (1993) investigated the use of New Zealand chironomids in paleoecology, there have been important developments in the taxonomy of this group in New Zealand. Boothroyd (1994, 1999, and 2002) and Martin & Forsyth (unpublished data) have improved the taxonomic resolution of the larvae from the sub-family Orthocladiinae and the genus *Chironomus* respectively. However, this taxonomic work has focused on identifying the live larvae, and is based on head-capsule *and* larval body features.

Another major objective of this thesis was to establish a reliable taxonomy for the sub-fossil chironomid larvae of New Zealand. The identification of sub-fossil chironomids is usually based on head-capsule morphology alone. The identification of some New Zealand chironomid species from fossil material is straight forward (e.g. *Cladopelma curtivalva*) as they have distinctive head-capsule features (e.g. the mentum) that are usually well preserved. Live chironomid larvae were collected during the course of this study to investigate the potential for identifying the nine cytologically distinct species of *Chironomus* identified by Martin and Forsyth. This research is important as this is the most common chironomid genus in New Zealand lakes.

Problems have also been identified with the taxonomy of the live larvae from other New Zealand taxa, particularly from tribe Macropelopini (Schakau, 1993). There is a discrepancy between the number of species described from this group as adults and the number that has been described from the larvae. My research also sought to identify any possible variation in the head-capsule morphology that could be attributed to interspecific variation.

9.2 Transfer function development

Exploratory data analysis (**Chapter 4**) revealed that February mean air temperature is the most important driver of chironomid species distribution in New Zealand lakes. The temperature effect was still dominant in the presence of other long environmental gradients, i.e. nutrients (TP, TN), production (chlorophyll *a*), and conductivity.

The temperature transfer function compares favourably with other chironomid-based temperature models from other parts of the world including Sweden (Larocque et al., 2001), Norway (Brooks and Birks, 2001) and Switzerland (Lotter et al., 1999). The New Zealand model performs quite well despite the apparent low taxonomic richness of the New Zealand fauna, and the small number of lakes used in the final temperature model (n = 31). In terms of absolute root mean squared error of prediction (RMSEP) the New Zealand weighted averaging (WA) model ($RMSEP_{jack}$ = 1.34 ºC) and weighted averaging-partial least squared (WA-PLS) ($RMSEP_{jack}$ = 1.28 ºC) is only slightly higher than the RMSEP from the Swedish training set ($RMSEP_{jack}$ = 1.13 ºC) (Larocque et al., 2001) that included 100 lakes and 42 taxa. The RMSEP as a proportion of the measured temperature gradient was high for the New Zealand transfer-functions compared to the European models. The RMSEPs for the temperature transfer-functions from this thesis were 18.4 and 17.5% of the length of the February mean temperature gradient.

The fact that the New Zealand temperature model is performing so well with a relatively limited dataset is encouraging. In **Section 9.2.1** I will discuss some possibilities for future research that will most likely result in an improvement in the performance of the New Zealand temperature transfer-function.

Identifying the dominant secondary environmental variable controlling chironomid distribution in New Zealand proved to be more difficult. There was a great deal of co-linearity in the lake production/chemistry training set, with the effect of conductivity and TN confounded. TN was selected as the dominant environmental variable based on the results of previous studies on the effect of salinity on New Zealand chironomid taxa. It appears that conductivity is not directly affecting the chironomid fauna in the lakes examined for this study. The transition from *Chironomus* spp. to *Chironomus* sp. a was observed at the upper end of the conductivity gradient (381µS/cm) but a study by Robb (1966) suggest that this transition should not occur until a conductivity transition that is hundreds of times higher. This evidence is also supported by data from training sets from other parts of the world (Walker et al., 1995) where similar taxonomic groups to those found in New Zealand do not show a significant response to conductivity until 1000 µS/cm. Future work should seek to disentangle the effect of nutrients and conductivity and this will be discussed in **Section 9.2.1**.

The TN transfer-function appears to be performing particularly well in comparison with other chironomid-based models for various indicators of lake trophic status from other parts of the world including TN (Brodersen and Anderson, 2000), total phosphorus (TP) (Brooks et al., 2001) and chlorophyll *a* (Brodersen and Lindegaard, 1999). The chironomid-based TN model also seems to outperform the existing New Zealand diatom based TP and chlorophyll *a* inference models (Reid, 2005).

9.2.1 Possible improvements to the transfer-function performance

The reliability of any transfer-function is dependent on many factors, including the quality of the environmental data and how accurately it represents the inherent variability of the variable in question. Perhaps the most important factor to consider is taxonomic resolution and consistency.

Taxonomy

An improvement in the taxonomy of the New Zealand chironomid taxa is probably the most important piece of work that could improve the performance of the chironomid inference models developed in this thesis. The taxonomy of the *Chironomus* spp. morphotype should receive priority as this taxon is the most common in New Zealand lakes. It has already been established that the genus *Chironomus* is represented by nine species in New Zealand (Martin and Forsyth unpublished data). My research has established that it is possible to reliably separate this genus into *Chironomus* sp. a and a morphotype (*Chironomus* spp.) that includes the other eight species on the basis of head-capsule morphology alone. This subdivision alone is significant as *Chironomus* sp. a is a species that is characteristic of eutrophic and/or saline water-bodies

Martin and Forsyth (unpublished data) have identified a great deal of variation in several important features (e.g. tooth arrangement on the mentum) between the eight species that make up the *Chironomus* spp. morphotype (**see Chapter 2, pp. 25**). However, at this stage there is not enough data to consistently attribute any of these features with an individual species. A study similar to that performed by Webb and Scholl (1985) measuring the variation of head-capsule morphological features for cytologically distinct species should be performed.

It may also be possible to separate the tribe Macropelopini into different species based on head-capsule morphology. Boothroyd (2000) lists nine described species belonging to the tribe Macropelopini from New Zealand. Nine species have been described in their adult form, but only one, *Gressittius antarcticus* (formally *Anatopynia antarctica*) has been formally described in its larval form and associated with the pupal and adult (imago) life stages (Freeman 1959). It

would be useful to collect a large sample of Macropleopini larvae from diverse environments and separate these into species using cytology. Rieradevall and Brooks (2001) have demonstrated that it is possible to identify subfossil Tanypodinae larvae based on the cephalic setation. The cephalic setation on head-capsules from the Macropelopini was examined as part of this thesis (**Chapter 2**, **Section 2.2**) but requires more work. My initial findings are encouraging, and there appears to be some variation in the cephalic setation that may or may not relate to inter-specific variation.

Environmental data

Possible improvements to the environmental data include obtaining more representative samples and collecting data from environmental variables that were not examined as part of this thesis. It was only possible to obtain "spot" measurements for the water chemistry and nutrient data for this thesis. Samples should be collected at least from summer, winter, spring, and autumn to capture the annual variation. Annual variation in such variables as lake production may prove to be important especially where there are multivoltine taxa in the chironomid assemblages. The use of annual average data for lake trophic status would also enable direct comparison with the current classification scheme for the trophic status of New Zealand lakes (Burns et al., 2000).

The collection of additional environmental variables may enable us to account for the unexplained variation in the chironomid assemblages between each lake. Many other variables have been identified from previous studies to be important controlling factors on chironomid distribution including, hypolimnetic anoxia (Little and Smol, 2001), substrate, and the presence of macrophytes (Langdon et al., 2006).

Training set expansion

The training sets for temperature and lake production/chemistry should be expanded to extend the range of the environmental gradient and to ensure that all parts of each environmental gradient have good representation. There is a distinct lack of lakes with a February mean air temperature between ca 11 and 13ºC and this should be rectified. The temperature training set should also be expanded to include a greater number of warmer (>14 ºC) lakes in undisturbed catchments. In the case of the production/chemistry training set there is a requirement for more highly productive lakes. Mesotrophic to Hypertophic lakes should also be sampled with a range of conductivities to facilitate the disentangling of the conductivity/lake trophy signal. Some of the more productive lakes in the central North Island would probably be suitable candidates.

Sampling more lakes may also enable a better representation of the chironomid taxa and therefore enable a better constraint on the factors that control the distribution of taxa that were rare in the dataset from this thesis. Some of taxa collected during this study were abundant, but were only present in one or two lakes (e.g. *Kiefferulus opalensis*), while other taxa (e.g. *Paucispinigera* sp.) were widespread but not abundant.

9.3 Transfer-function application

9.3.1 Temperature

The temperature transfer-function appears to be producing reasonable reconstructions in comparison temperature estimates from other proxies, including plant macrofossils (Soons and Burrows, 1978) and the beetles (Marra et al., 2006). The maximum amount of cooling achieved during the MIS 2/3 (26.6- 24.5 ka BP) transition was the key question. I wanted to determine whether the climate was cold enough to exclude canopy trees (e.g. *Nothofagus*) from this site and to estimate the altitude of the tree-line.

During the development and application of the temperature model two possible problems with the temperature transfer-function became apparent. All of the inference models have a tendency to under-predict warmer (> 14ºC) and over-estimate cooler (< 14 ºC) temperatures. This tendency is regarded as an inherent feature of WA-PLS based models (ter Braak and Juggins 1993; Lotter et al. 1997). Another problem is the relatively large sample specific errors produced for this reconstruction. The $RMSEP_{jack}$ for the WA (tolerance down-weighted) temperature inference model (1.28 ºC) was the lowest of the three methods (WA-PLS, WA, PLS) (**Chapter 6**, **p. 131**) but the sample specific errors for the WA-based reconstructions averaged 1.7 ºC and reached 1.86 ºC (**Chapter 7**, **Fig. 7.6**). Birks (1998) states that fossil samples with poor analogues in the modern training set are likely to produce the most unreliable reconstructions. A sample with a poor analogue would include taxa that are poorly represented (< 10% occurrences) or do not exist at all in the modern training set.

The Lyndon Stream record is dominated by four taxa: *Chironomus* spp., Macropelopini, *Naonella kimihia*, and *Corynocera* sp.. All of these taxa are common in the modern training set. Birks (1998) also states that problems may arise when there is a strong representation of one or a few taxa in fossil assemblages. This is the case with the Lyndon Stream record where *Chironomus* spp. and *Naonella kimihia* are the most abundant taxa. Again, the subdivision of the *Chironomus* spp. morphotypes may result in a reduction of the sample specific errors.

It appears that *N. kimihia* does actually represent one species with a wide temperature tolerance. *N. kimihia* is present in the modern training set at temperatures as cool as 9.7 ºC. As *N. kimihia* is present for the entire Lyndon Stream record, I assume that the summer temperature did not fall below this value. This corresponds to a temperature that is 0.5 ºC cooler than the maximum inferred cooling from the WA model at 150 cm depth (**Chapter 7**, **Fig. 7.6B**), i.e. a maximum of 4.2 ºC cooling compared to the modern February mean at this site.

Such a temperature depression would still not explain the low concentrations of canopy tree pollen from sites around New Zealand during the MIS 2/3 transition. Wardle (1985) states that the climatic tree limit in New Zealand represents the maximum altitude to which summer conditions permit the shoots of tall woody plants to grow and mature sufficiently to withstand winter. A cooling of up to 4.2 ºC would therefore result in a depression of the tree-line by 700m. At Lyndon Stream (700 m asl) this would mean a drop of the tree-line from ~ 1300 to 600m. Consequently, the effect of other environmental variables must be invoked to explain the minimal concentration of canopy tree pollen in New Zealand records that span the MIS 2/3 transition. Altered CO_2 regimes, fire, drought, invasion of cold maritime polar air masses, and strong winds have been cited as possible causes for the lack of forest cover during the New Zealand LGM (McGlone and Bathgate, 1983; McGlone, 1985, 1988).

The chironomid-based temperature reconstructions highlight the need to investigate the variability of other environmental variables during the last glaciation.

9.3.2 Total nitrogen

The total nitrogen (TN) transfer-function is producing reconstructions that tend to agree with other proxies (e.g. bryozoan stomatoblasts and Trichopteran remains) and actual observations of changes in the condition of Alexander Lake through time (**Chapter 7**). The sample specific error for each individual sample is large compared to the overall trend, but it appears that the trend does mirror reports of the change in lake conditions after local deforestation. This is in keeping with the recommendation of Brooks and Birks (2001), who suggest that interpretation of inferred environmental values should be a combination of the individual inferences (for short-term changes) and of the LOESS smoothed curve (for long-term changes).

When examining the individual reconstructions, it may be possible to talk in terms of the probability that the lake was in a certain condition. For example for the reconstructions using all of the taxa, there is a 0% probability that Alexander Lake was eutrophic prior to 1965 (**Fig. 8.9**, **Chapter 8**). After local deforestation there is a small (for the model with all taxa) and 0%

probability (for the model with only significant taxa) that Alexander Lake was oligotrophic. In the case of Alexander Lake the information from other proxies provided useful information that supported the general trend of eutrophication predicted by the chironomid reconstructions.

The TN model compares favourably to chironomid-based inference models for lake trophic variables (including TN) from other parts of the world, despite the fact that spot TN measurements were used. Most of the other studies have used either mean summer values (e.g. chlorophyll *a*; Brodersen and Lindegaard, 1999) or annual mean values (e.g. total phosphorus; Brookes et al., 2001). Future work should investigate using mean values for lake trophic variables spanning similar time spans to see if this improves model performance.

The other interesting feature of the TN transfer function was the improvement of the model performance when the non-significant taxa (those with a null response model to the target variable) were removed from the training set (**Table 6.8**, **Chapter 6**). Conversely, the removal of the non-significant taxa did not improve the performance of the temperature transfer function. Birks (1998) mention that (surprisingly) it is often the case that the most robust inference models based on WA or WA-PLS are those that include all of the taxa. The WA and WA-PLS TN models including only the significant taxa (n = 6) produced sample specific errors that were consistently lower than the WA, WA-PLS and PLS based models including all of the taxa. Other studies (e.g. Racca et al., 2004) have shown that the removal of non-significant taxa from diatom training sets improves transfer-function performance. Although other studies have investigated the significance of individual chironomid species response to the environmental variable of interest (e.g. Brooks et al., 2001) there have been no other attempts to assess the performance of chironomid-based inference models after non-significant taxa have been removed. The low number (6) of taxa that display a significant response to TN may be increased by expanding the number of lakes in the training set.

9.3.2 Chironomids as a proxy in coastal lakes

The fact that many of New Zealand's shallow coastal brackish lakes and lagoons are highly productive (eutrophic-hypertrophic) (Jeppesen et al., 2000; Schallenberg and Burns, 2003; Woodward and Shulmeister, 2006; Canterbury Regional Council unpublished monitoring data) provided an impetus to investigate the potential for the use of chironomids as a proxy for anthropogenic eutrophication in these settings. The results from the Lake Forsyth study (**Chapter 3**) coupled with the results of the exploratory data analyses (**Chapter 5**) and a study performed by Robb (1966) indicate that the chironomids will not be useful proxies for trophic status in saline environments. This is because *Chironomus* sp. a is the dominant taxon in both

eutrophic freshwater lakes and saline water-bodies of varying productivity. However, if chironomids are applied to coastal water bodies that experience prolonged fresh-water *or* saline phases, chironomids will be suitable for pinpointing the trophic conditions during the fresh-water phases. This appears to be the case with some New Zealand barrier blocked lakes (Forsyth and Ellesmere) that have been intermittently connected to the ocean in the past.
Other proxies will be more useful for providing records of changes in lake nutrients and production that span both saline and fresh-water phases. This will be discussed in the following section.

9.4 Other possibilities for future research

9.4.1 Validation of transfer-functions with monitoring records and climate data.

Future research should test the performance of the chironomid-based transfer functions for TN and temperature against actual monitoring records and climate records respectively. Previous studies from elsewhere in the world have compared chironomid-based reconstructions for trophic indicators (e.g. chlorophyll *a*; Brodersen et al., 2001) with actual lake monitoring data. Larocque and Hall (2003) compared chironomid-based temperature reconstructions with an 87 year climate record from northern Sweden. Studies such as this provide a true indication of the reliability of the transfer-functions and the performance of different transfer-functions based on different models (WA, WA-PLS, PLS) or taxon deletion criteria.

There are several lakes in the North Island that would be good candidates for a test of the TN transfer-function. There is good monitoring data from Lake Rotorua (TN, TP, chlorophyll *a*) that extends back to 1967 (Environment Bay of Plenty, unpublished data). Ideally, the temperature transfer function should be tested in a lake that is situated in an un-disturbed catchment. The National Institute of Water and Atmosphere Research (NIWA) Climate Database contains temperature records with a reasonable coverage of the New Zealand land-mass that extend back to the 1920s. Site temperature trends were documented for the period 1920–1990 by Salinger et al. (1992a, b) for records from 21 stations with rigorously quality controlled measurements. These showed increases in annual mean temperatures between the decades 1941–1950 and 1981–1990 for the North Island of 0.8°C, and 0.7°C for the South Island. Such a small change in temperature is within the RMSEP of the temperature transfer functions (**Chapter 6**) which have a minimum $RMSEP_{jack}$ of 1.28 ºC. This means the error range for temperature estimates is 2.56 ºC. The improvements suggested in **Section 9.2.1** should result in a reduction of the RMSEP. However, even some particularly robust models from other parts of the world have

$RMSEP_{jack}$ of 0.9 ºC (Brooks and Birks, 2001), which is equivalent to a range of 1.8 ºC. The results from other studies have shown (Larocque and Hall, 2003) that even with an error range of this magnitude the overall trends in the chironomid-based reconstructions closely match those in the actual meteorological records.

9.4.2 Proxies for production in coastal waterways

The chironomids show great potential for long-term reconstructions of the trophic status for New Zealand's freshwater lakes. However, the results from the Lake Forsyth study (**Chapter 3**) suggest that other proxies should be explored to be used in coastal brackish lakes. The diatom nutrient (TP, dissolved reactive P) and production (chlorophyll a) transfer-functions of Reid (2005) show potential for this setting, but the confounding effect of lake production and conductivity needs further investigation (see **Chapter 4**, **p. 62**). It may be possible to use a subset of the diatom taxa that are not sensitive to changes in conductivity. Dinoflagellate cysts have also been shown to be useful indicators of cultural eutrophication (Dale et al., 1999). Baldwin (1987) revealed that a reasonably diverse dinoflagellate taxa (17 species) in the surface sediments from the Marlborough Sounds in the South island.

Studies from other parts of the world have demonstrated the value of some other proxies that may also be useful in New Zealand estuaries, coastal lagoons and barrier-blocked lakes. Turner et al. (2006) used a suite of biological and geochemical proxies, including sediment biogenic silica (a proxy for diatom production), carbon, nitrogen, phosphorus and algal pigment concentrations to reconstruct the nutrient history in the Charlotte Harbour estuary in Florida.

9.5 Summary

This thesis has resulted in the development robust chironomid-based transfer-functions for air temperature and total nitrogen (TN). The New Zealand transfer-functions for both variables compare favourably with chironomid-based transfer-functions for equivalent variables from elsewhere in the world, and diatom-based transfer-functions for nutrients and lake production from New Zealand. The application of the temperature and TN transfer-functions provided insight into New Zealand climate conditions during the last glacial (temperature), and served as a test for the reconstructions (both variables).

Chironomid-based Temperature reconstructions from Lyndon Stream indicate a maximum cooling of ca 4 ºC between 26.6 and 24.5 ka BP which is consistent with estimates based on

beetles and plant macrofossils. A cooling of 4 ºC is insufficient to explain the lack of canopy tree pollen in many New Zealand pollen records at this time. Other environmental parameters additional to temperature are contributing to limit the expansion forest cover during this time. This study highlights the potential of chironomids based reconstructions to extend and amplify the late Quaternary paleoclimate history of New Zealand.

The chironomid-based TN reconstructions produced a pattern of rapidly deteriorating water-quality in a small doline following the removal of re-generating native forest immediately surrounding the lake. The overall trend and timing of eutrophication was consistent with other biological proxies and actual observations of changes in lake water quality.

The chironomid-based transfer-functions provide a valuable new tool the study of long-term climate variability and improving our understanding of the response of aquatic ecosystems to long-term natural and human induced environmental change. I have identified some possibilities for future research which should improve the performance of these transfer-functions. The improvement of the chironomid taxonomy and the expansion of the training set should be the highest priorities.

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APPENDIX A: IDENTIFICATION KEY FOR THE FOSSIL CHIRONOMIDAE OF NEW ZEALAND

1 Head-capsule with mentum(Mt) as depicted in Fig. 1, with or without ventromental plates (Vmp) 6
2 Head-capsule elongate ligula (L) present (Fig. 2)- 3

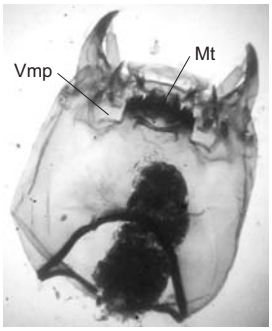


Fig. 1

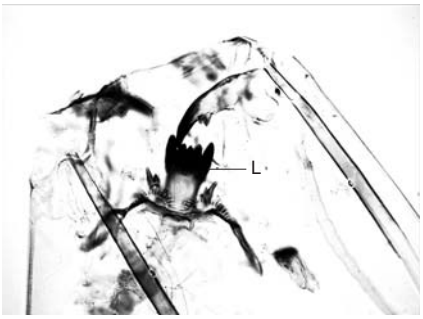


Fig. 2

3(2) Head-capsule more elongate longitudinally, teeth absent on the mentum, ventral pore anterior to the sub mental seta (SSm)(Fig.3).
Spinules may be present on the surface of the head-capsule (Fig. 3) - 4

Fig. 3

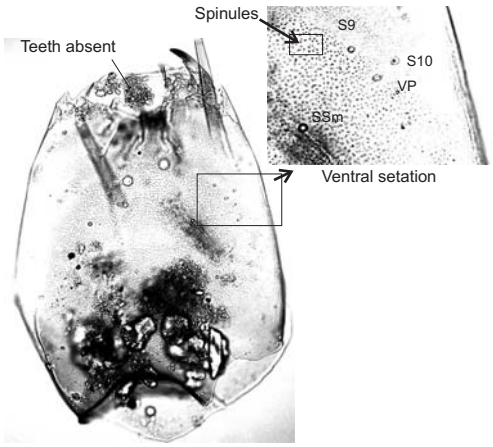
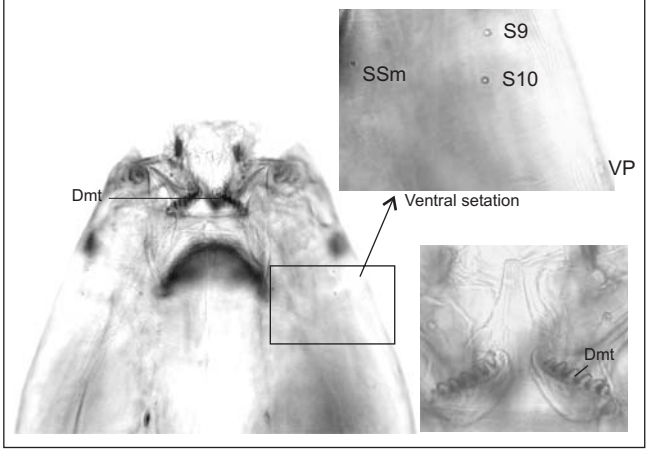


Fig. 4



Teeth present on the mentum on two distinct dorsomental plates, dorsomental teeth (Dmt). SSm in between or posterior to the S9 and S10. VP posterior to SSm Surface of head-capsule smooth: **Macropelopini (Fig.4)**

4(3) Maxillary palp with more than one basal segment (when preserved) (Fig. 6), ventral setae as in Fig. 3. Ligula strongly pigmented with 5 teeth. Outer teeth longer than inner teeth (Fig. 5). Pecten hyperpharaynis (Ph) as in Fig. 5. Paraligula (Pl) bifid: ***Ablabesmyia mala*** **(Fig. 3,5 and 6)**

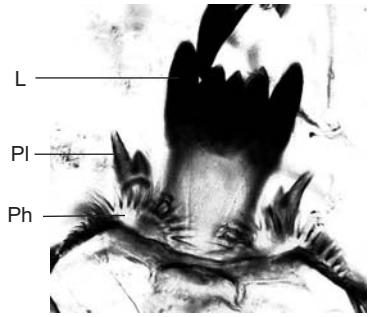


Fig. 5

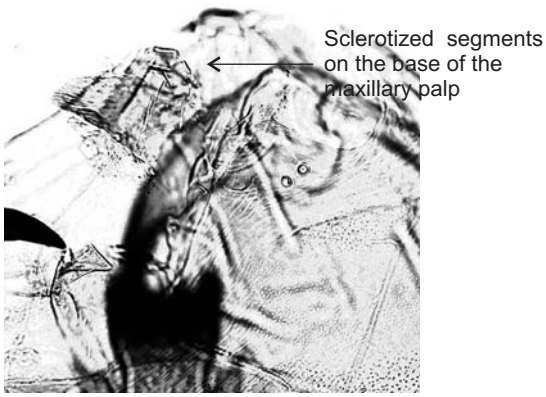


Fig. 6

Maxillary palp with a single basal segment (when preserved)- -5

5(4) Ligula 5 teeth, short central tooth outer teeth approximately the same length. Para ligula with forked apex and basal accessory tooth as in Fig. 7 ***Zavrelimyia harrisi*** **Freeman**

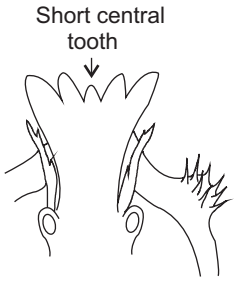


Fig. 7

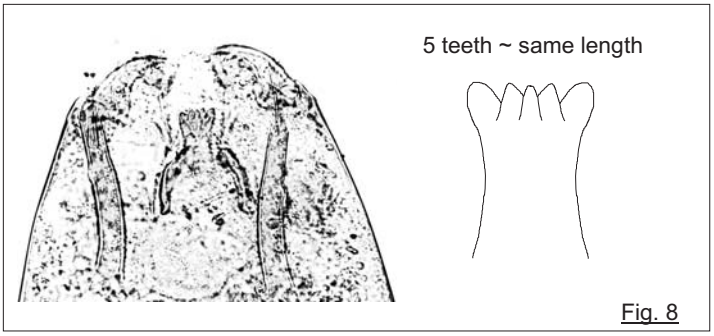


Fig. 8

Ligula 5 teeth approximately equal length. Paraligual bifid without accessory tooth Fig. 8 ***Larsia***

6(1) Well developed ventromental plates (Fig. 9) - 7
Ventromental plates less prominent (Fig. 10 a & b)- -17

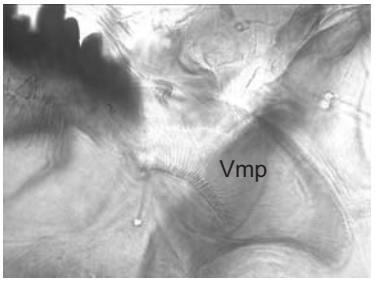


Fig. 9

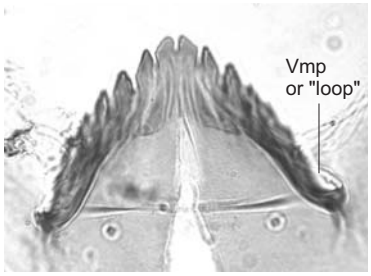


Fig. 10a

Fig. 10b

7(6) Ventromental plates broad and flat as in Fig. 9 - 8
Ventromental plates more elongate as in Fig. 11 - 15

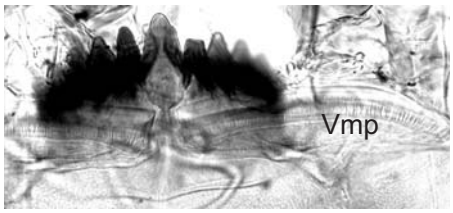


Fig. 11

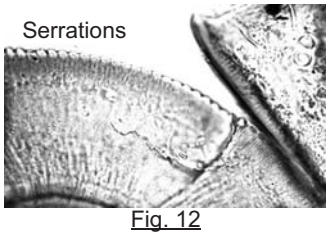


Fig. 12

8(7)Margin of Vmp serrated (Fig. 12) - 9
Margin of Vmp smooth as in Fig. 9 - 10

9(8) Median tooth trifid as in Fig. 13. First laterals equal to or longer than the median tooth. median tooth usually tapered towards the base 6 laterals ***Kiefferuls opalensis*** **(Fig. 13)**
Single middle tooth, 7 laterals ***Parachironomus*** **(Fig. 14)**

10(8) Middle tooth trifid as in (Fig. 13) - 11
Middle tooth double -13
Single central tooth - 14
5-8 small middle teeth, 8 laterals ***Xenochironomus*** **(Fig. 15)**

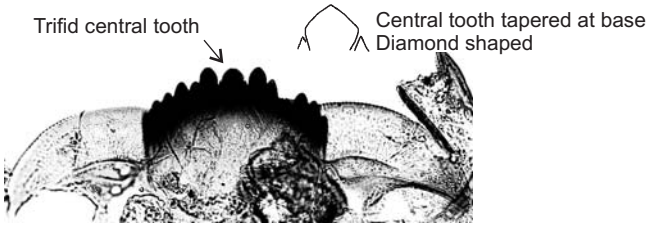


Fig. 13

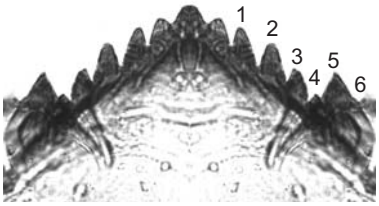


Fig. 16

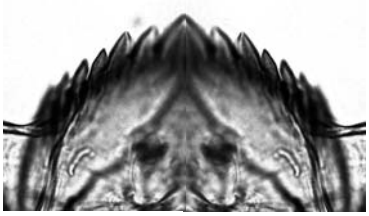


Fig. 14

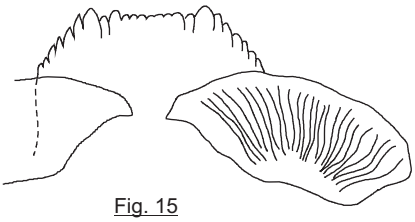


Fig. 15

11(10) 6 pairs of laterals. First laterals equal to or longer than the middle tooth (Fig. 17) - - - - - - - 12
6 pairs of laterals. Fifth large, fourth and sixth reduced **Cladopelma curtivalva** (Fig. 16)

12(11)Vmp striations fine and numerous (Fig. 18). Gular area usually very dark (Fig. 19c)
***Chironomus* sp. a**
Vmp striations more coarse and less numerous (Fig. 20)
Gular region pale to darkened (19 b & c) ***Chironomus* spp.**

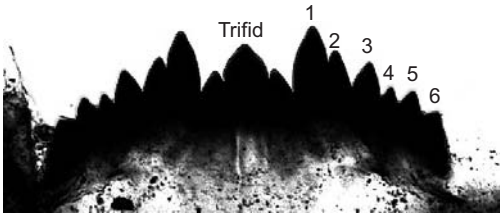


Fig. 17

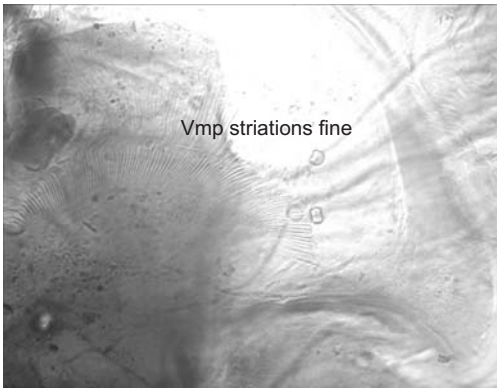


Fig. 18

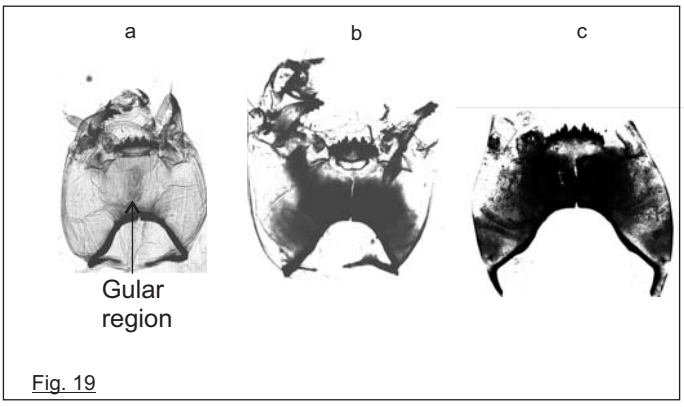


Fig. 19

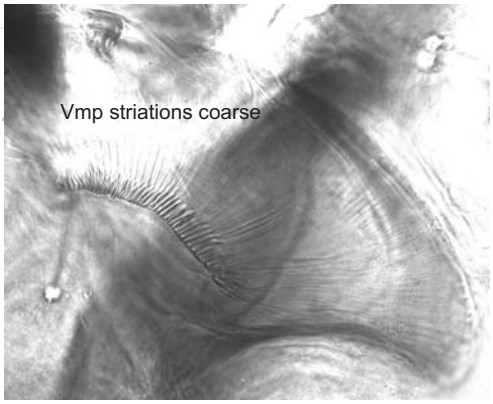


Fig. 20

13(10) Middle teeth large, 7 laterals. 1st lateral small, 2nd lateral almost as long as middle teeth ***Polypedilum*** **(Fig. 22)**
Middle teeth very small, 7 laterals ***Paucispinigera*** **(Fig. 21)**

Fig. 21

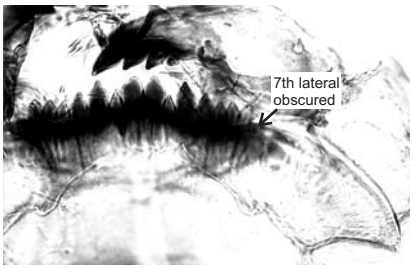


Fig. 22

14 (10) 6 laterals on the mentum. Second lateral short. Vmp similar to *Tanytarsus* but broader ***Pseudochironomus*** **(Fig. 23)**

15 (7) Mentum with 5 laterals - - -

17 (6) Single central tooth on the mentum - - -

20(18) Mentum profile convex. Middle tooth broad.1st laterals ~ same length as middle tooth
Long apical tooth on the mandible. Seta subdentalis on molar.
Axis of symmetry of laterals 3,4, and 5 all converge with axis of mentum ***Smittia*** (Fig. 33)

Mentum profile convex. Middle tooth extends well beyond the 1st laterals. Mola on mandible swollen without a seta subdentalis (Ss). Axis of symmertry of laterals 3,4,and 5 diverge from axis of mentum **Orthoclad species J**

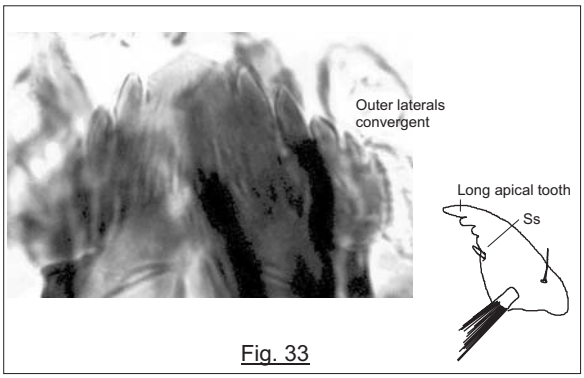


Fig. 33

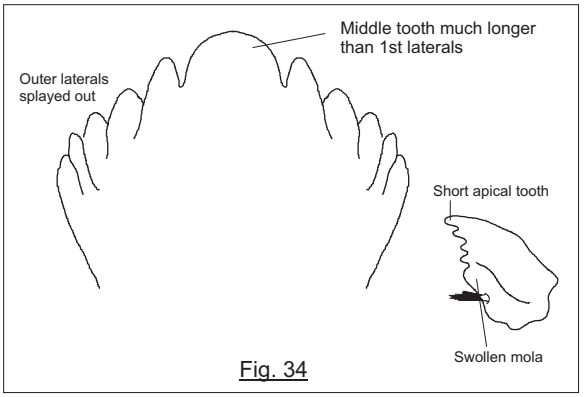


Fig. 34

21(18) Mentum profile concave. Mentum strongly pigmented. Laterals appear darker than central part of mentum (Fig. 35 a & b). Mandible: one apical tooth 6 distinctive accessory teeth Fig. 35e. Antenna with 5 segments (Fig. 35c) Head-capsule with thick "collar" (Fig. 36). Premandible simple and bifid (Fig. 35d) **Orthoclad species 1/6**

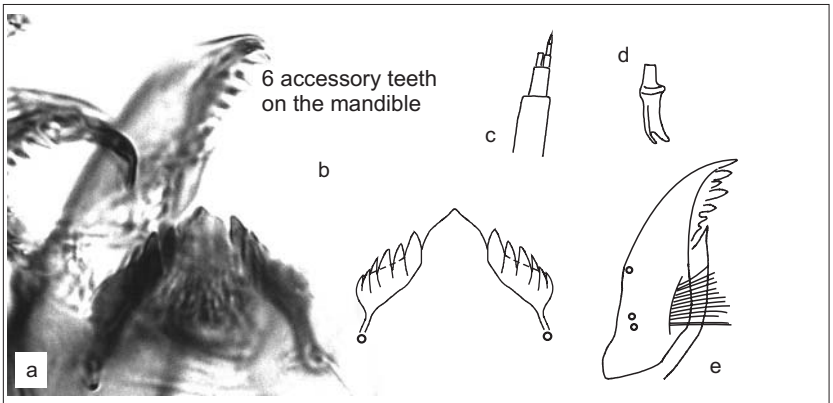


Fig. 35

Fig. 36

22(21) 1st laterals on the mentum ~0.5X the width of the central tooth.
1st laterals <0.5X the width of the central tooth. Inner margin of mandible serrated (Fig. 37b)
Crictocopus Aucklandensis **(Fig. 37a and b)**

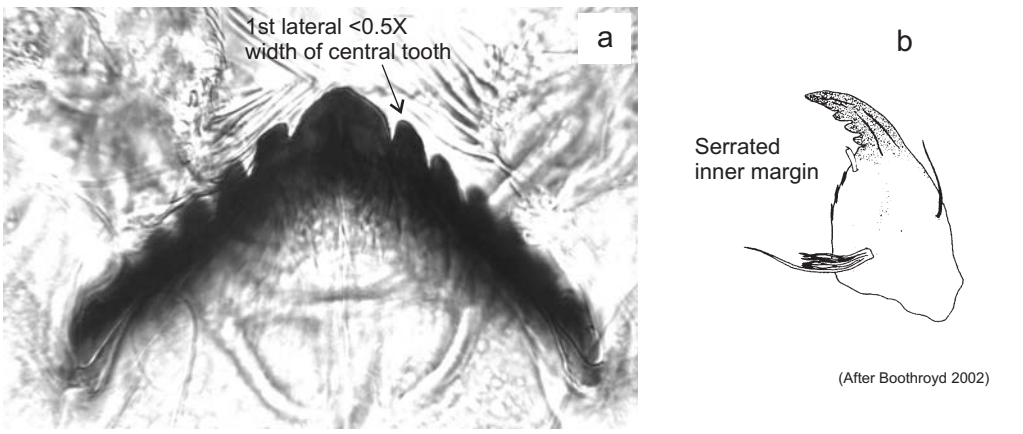


Fig. 37

23(22) Teeth of the mentum uniformly and heavily sclerotized, 1st laterals ~0.5X width of middle tooth. Axis of symmetry of laterals parallel to that of the middle tooth Inner margin of mandible smooth, outer margin rugose. 1st and 2nd laterals ~ same size 3rd lateral larger than 4,5, and 6. 6th lateral much smaller than 3,4, and 5. ***Paratrichocladius pluriserialis*** (Fig. 38a and b)

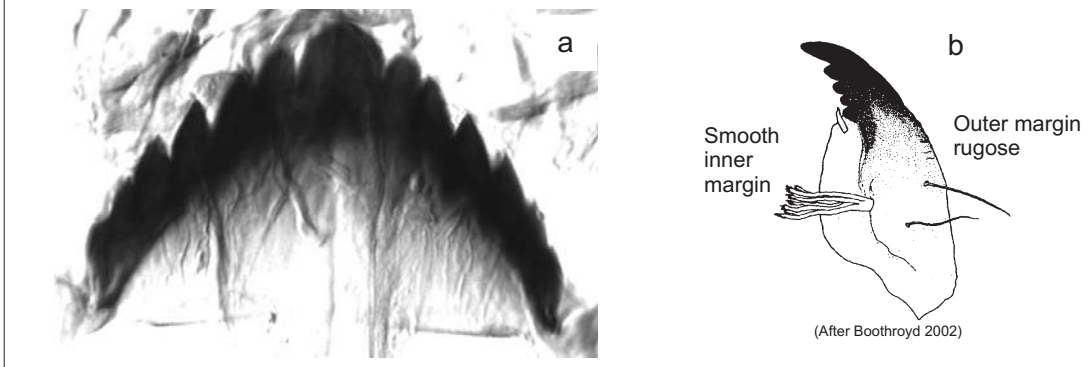


Fig. 38

Pigmentation of middle portion of the mentum lighter than laterals 3-6. 1st laterals ~0.5X width of middle tooth. Axis of symmetry of laterals convergent to the axis of the cental tooth Inner margin of the mandible serrated ***Crictocopus zealandicus*** (Fig. 39a and b)

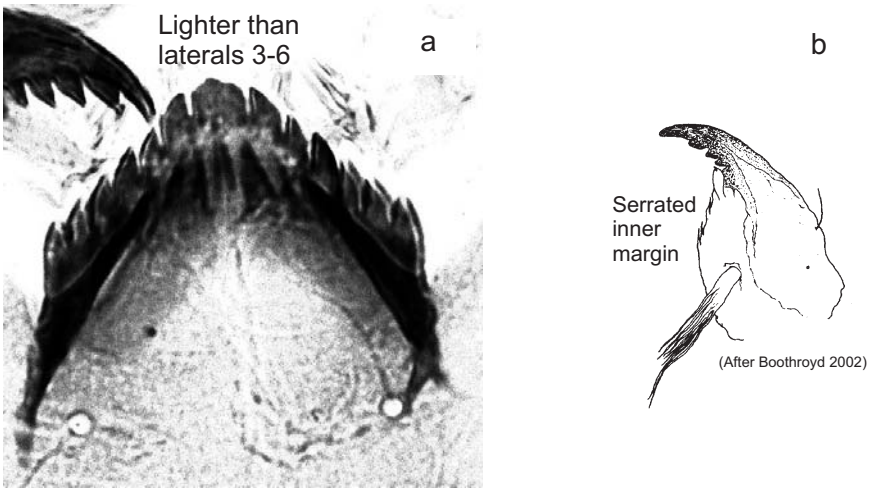


Fig. 39

Median tooth <1.5x wider and >1.5x higher than 1st lateral teeth.
Inner and outer margin with serrations. ***Crictocopus planus (***Fig. 40a and b)

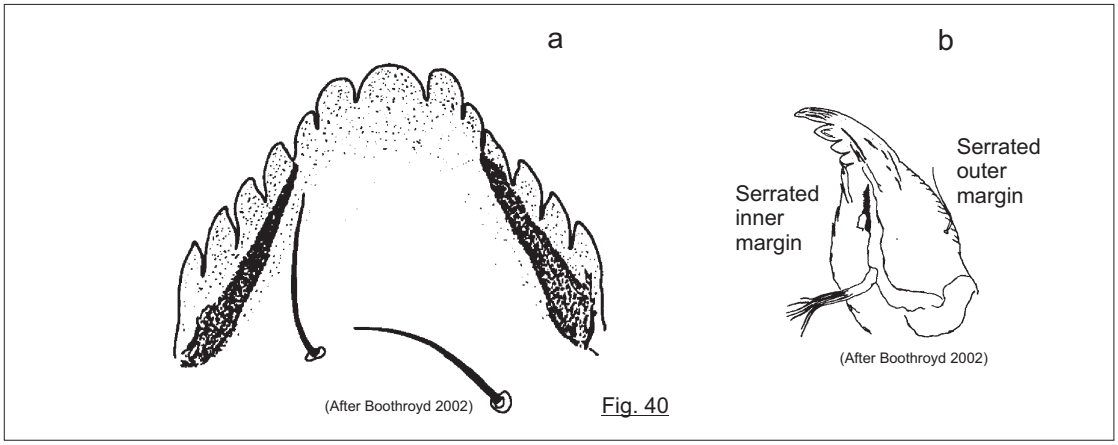


Fig. 40

24(17) 3 laterals on the mentum - - -

27(24) Ventromental 'loops' not present - - -

Fig. 48

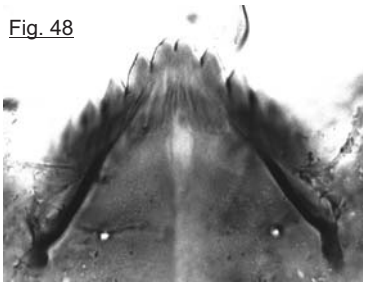


Fig. 49

Central teeth much wider than the first laterals. 5th lateral smaller than 3 and 4. 1st laterals appear more isolated from the central teeth than for Orthoclad D. Prominent ridges absent. **Orthoclad species G "Stockton"** (Fig. 49)

30(28) Central teeth pointed and partially connected. 4th and 5th laterals ~ same size and much smaller than the other laterals. Sides of central bifid teeth at angles to the axis of symmetry of the head-capsule:***Orthoclad species C "Claspers"*** **(Fig. 50)**

Similar to above except laterals 3,4, 5 and 6 are ~ the same size and smaller than 1 an 2. Sides of central bifid teeth ~ perpendicular to the axis o symettry of the head-capsule **Orthoclad species I (Fig. 51)**

Fig. 50

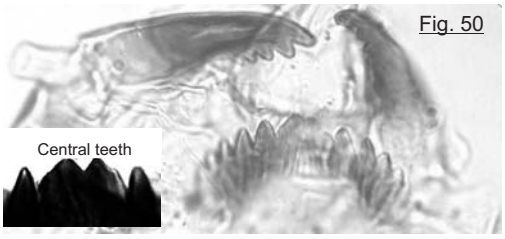
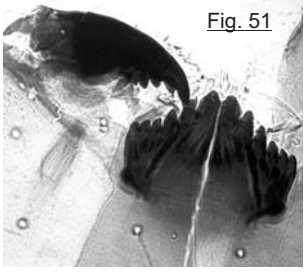


Fig. 51



31(27) Profile of mentum convex - - -

33(17) 7 laterals. 2nd lateral about as tall as 1st. Median larger than 1st lateral. Mandible as depicted in Fig. 54; 7 teeth, 1st inner tooth longer. ***Parochlus*** **(Fig.54)**
Parochlus B Similar to Parochlus. Mentum much darker in the centre.

8 laterals. Median ~ same size as 1st and 2nd laterals. Mandible as depicted in Fig. 55b, 7 teeth, 1st and 2nd teeth ~ same size. ***Podonomus*** **(Fig. 55)**

Fig. 54

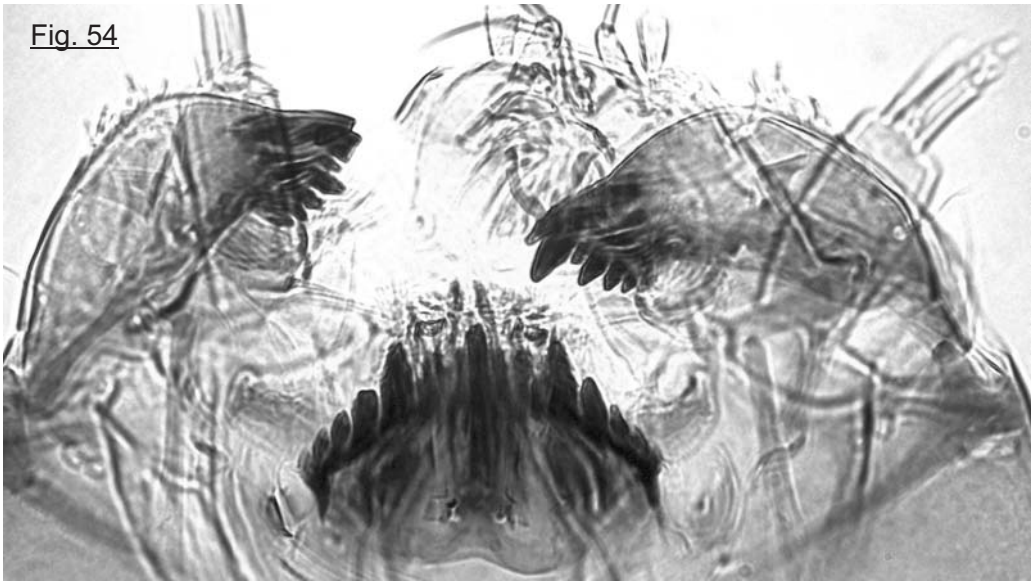
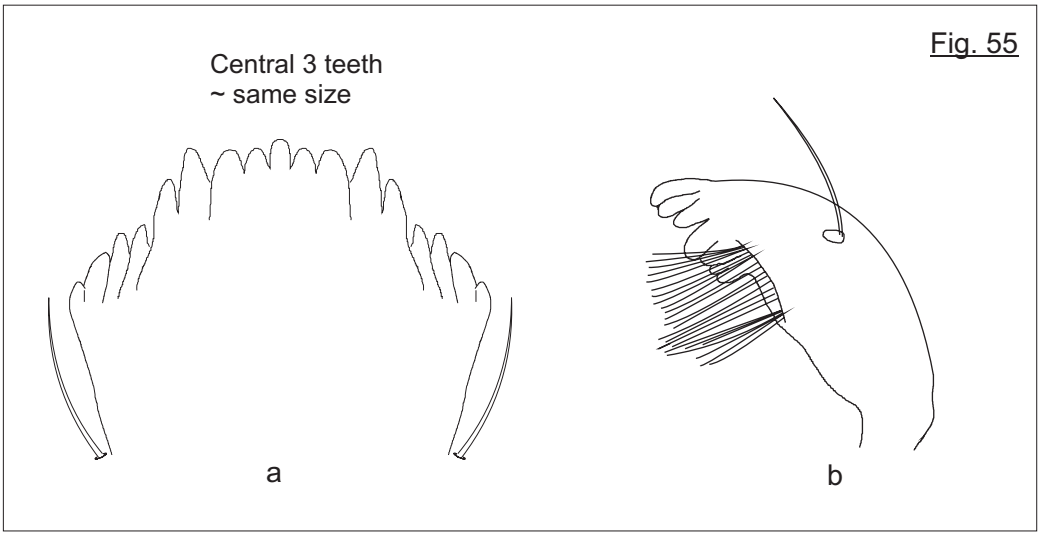


Fig. 55



APPENDIX B: LIMNOLOGICAL AND CATCHMENT DATA FOR THE NEW ZEALAND TRAINING SET

B1: Complete set of lake data part 1.

Lake nr	Location	Lat (°S)	Long (°E)	Altitude (m)	Feb Mean (°C)	Water temp. (°C)	Lake Area (Km^2)	Depth (m)	Secchi Depth (m)	Cond ($\mu S\ cm^{-1}$)	NOx-N (mg/L)
1	**Lake Rotorua N**	38.04	176.16	280	17.8	17.0	79.780	20.50	2.030	200.00	0.0005
2	**Lake Rotoehu**	38.01	176.31	295	17.6	20.5	8.110	10.00	2.040	150.00	0.0180
3	**Lake Rerewhakaaitu**	38.17	176.29	435	16.8	16.8	7.470	14.00	4.500	30.00	0.0040
4	**Lake Okaro**	38.17	176.23	412	17	19.1	0.280	16.00	2.440	91.90	0.0110
5	**Lake Tutira**	39.13	176.53	150	18.1	19.1	1.470	40.00	5.600	127.88	0.0430
6	**Lake Dudding**	40.06	175.16	86	17.5	18.3	0.130	12.00	2.600	125.30	0.0280
7	**Iron Lake**	41.06	172.36	1463	10.2	13.9	0.068	21.00	8.100	17.70	0.0220
8	**Lake Sylvester**	41.06	172.37	1333	10.9	12.8	0.266	24.20	6.900	26.70	0.0190
9	**Little Sylvester Lake**	41.06	172.37	1333	10.7	13.5	0.076	14.00	4.000	42.40	0.0210
10	**Rainbow Skifield W**	41.52	172.51	1690	9.8	13.8	0.052	10.10	9.500	10.10	0.0190
11	**Rainbow Skifield E**	41.53	172.52	1479	10.5	13.8	0.028	4.50	4.500	26.30	0.0180
12	**Lake Sedgemere**	42.08	172.54	1008	12.9	14.7	0.080	1.30	1.300	30.90	0.0040
13	**Princess Bath**	42.11	172.41	1757	9	10.2	0.070	15.50	10.500	13.40	0.0180
14	**Lake Rotorua S**	42.24	173.34	20	17.3	28.8	0.550	2.08	0.380	185.00	0.0188
15	**Horseshoe Lake**	42.35	172.31	468	15.4	18.0	0.040	10.30	3.700	83.70	0.0131
16	**Lake Taylor**	42.46	172.13	588	14.1	13.2	1.850	35.00	6.650	53.00	0.0011
17	**Lake Mason**	42.44	172.10	329	14.1	13.2	1.000	37.00	6.400	61.90	0.0009
18	**Lake Sheppard**	42.45	172.15	587	14.6	14.6	1.150	17.00	1.450	56.40	0.0003
19	**St Annes Lagoon**	42.46	173.16	33	17.1	25.9	0.200	1.00	0.245	340.50	0.0088
20	**Mill**	42.55	172.55	146	16.6	21.1	0.060	2.70	0.500	256.00	0.0075
21	**Lake Greta**	42.57	172.58	183	16.3	19.8	0.020	3.10	0.440	173.60	0.2440
22	**Glen**	43.01	172.47	78	16.8	19.2	0.070	1.40	0.177	381.00	0.0058
23	**Hut**	43.02	172.46	71	16.9	17.4	0.100	5.00	0.195	251.00	0.1161
24	**Lake Pearson**	43.06	171.46	611	14.6	16.0	1.790	15.00	4.450	44.90	0.0018
25	**Mystery Tarn**	43.12	171.34	854	13.3	13.3	0.020	8.00	3.800	6.90	0.0061
26	**Lake Evelyn**	43.15	171.32	580	14.7	17.5	0.150	3.00	3.000	55.80	0.0060
27	**Lake Heron**	43.29	171.10	691	13.7	13.0	6.300	36.00	5.600	51.10	0.0148
28	**Lake Camp**	43.36	171.03	674	13.8	17.4	0.490	13.00	2.100	69.60	0.0041
29	**Lake Roundabout**	43.37	171.05	653	13.9	18.0	0.130	0.74	0.740	57.90	0.0041
30	**Lake Emma**	43.38	171.06	655.5	13.9	24.4	1.550	2.20	0.720	64.10	0.0048
31	**Groynes**	43.27	172.36	25	16.8	21.6	0.018	1.25	1.250	62.40	0.0065
32	**Lake Forsyth**	43.48	172.44	20	17	17.0	5.620	1.60	0.660	1180.00	0.0806
33	**Lake Middleton**	44.16	169.50	526	15.5	17.7	0.230	4.50	2.300	21.80	0.0040
34	**Red Lagoon**	44.18	169.52	589	15.2	18.9	0.160	1.25	1.200	37.60	0.0042
35	**Swan Lagoon**	44.18	169.55	576	15.2	19.4	0.345	1.40	0.660	95.30	0.0054
36	**Avon**	44.23	169.38	734	14.4	21.3	0.100	1.50	1.400	68.30	0.0040
37	**Lake Sylvan**	44.42	168.19	383	14.3	17.1	0.720	19.15	3.800	45.00	0.0040
38	**Lake Harris**	44.43	168.10	1231	9.6	7.4	0.250	40.00	8.000	16.13	0.0040
39	**Lake Mackenzie**	44.45	168.10	885.5	11.4	8.3	0.200	34.20	11.500	15.52	0.0040
40	**Gertrude Saddle**	44.44	168.01	1371.5	8.4	6.1	0.010	2.90	2.900	68.20	0.0040
41	**Lake Howden**	44.49	168.08	684	12.4	11.9	0.100	9.40	2.500	102.00	0.0040
42	**Lake Hayes**	44.58	168.48	329	15.8	14.5	2.030	31.00	4.750	141.46	0.0005
43	**Lake Johnson**	45.00	168.43	406	15.4	15.1	0.200	28.30	1.940	216.00	0.0040
44	**"Sugarbowl Tarn"**	45.03	168.49	1799.5	8.2	13.7	0.014	6.15	6.200	24.30	0.0040
45	**Lake Alta**	45.04	168.48	1882	8.2	8.1	0.130	36.10	9.850	15.38	0.0040
46	**Lake Mistletoe**	45.12	167.49	207	14.6	14.1	0.100	13.65	3.500	57.70	0.0040
	Max	45.12	176.53	1882	18.100	28.8	79.780	40.00	11.500	1180.00	0.2440
	Min	38.01	167.49	20	8.200	6.1	0.010	0.74	0.177	6.90	0.0003
	Mean	42.63	171.56	665	14.093	16.2	2.686	13.65	3.629	114.18	0.0179
	Median	43.04	172.14	583.5	14.600	16.9	0.180	10.20	2.750	59.90	0.0051
	SD	1.94	2.48	532.3	2.874	4.6	11.780	12.55	3.020	182.59	0.0398

B2: Complete set of lake data part 2.

Lake nr	Location	React P (mg/L)	TN (mg/L)	TP (mg/L)	Chla (µg/L)	TC (mg/L)	DIC (mg/L)	DOC (mg/L)	Ca (mg/L)
1	Lake Rotorua N	0.0220	0.5905	0.0660	32.10	-	-	-	-
2	Lake Rotoehu	0.0230	0.7100	0.0600	25.00	-	-	-	-
3	Lake Rerewhakaaitu	0.0010	0.3400	0.0100	3.60	-	-	-	-
4	Lake Okaro	0.0164	0.8765	0.0283	5.79	-	-	-	-
5	Lake Tutira	0.0010	0.1047	0.0069	3.82	-	-	-	-
6	Lake Dudding	0.0226	1.3185	0.0589	19.11	-	-	-	-
7	Iron Lake	0.0050	0.0700	0.0100	0.50	3.700	1.500	2.100	2.200
8	Lake Sylvester	0.0030	0.0500	0.0300	0.40	4.400	2.500	1.800	3.300
9	Little Sylvester Lake	0.0030	0.0900	0.0300	0.40	7.300	4.300	3.000	5.900
10	Rainbow Skifield W	0.0030	0.0800	0.0100	0.70	2.900	1.100	1.800	1.200
11	Rainbow Skifield E	0.0030	0.0600	0.0300	0.20	4.300	2.700	1.600	4.800
12	Lake Sedgemere	0.0375	0.3996	0.0427	0.50	10.597	4.103	6.494	3.447
13	Princess Bath	0.0030	0.1200	0.0100	2.30	2.600	1.400	1.100	2.200
14	Lake Rotorua S	0.0269	6.0750	0.4529	15.30	56.987	2.850	54.137	5.887
15	Horseshoe Lake	0.0087	0.4726	0.0100	0.40	16.076	8.132	7.944	10.693
16	Lake Taylor	0.0030	0.1434	0.0069	2.27	-	-	-	-
17	Lake Mason	0.0009	0.1054	0.0100	1.11	-	-	-	-
18	Lake Sheppard	0.0046	0.2821	0.0223	8.10	-	-	-	-
19	St Annes Lagoon	1.9701	2.7099	2.8038	7.30	65.472	19.094	46.377	20.329
20	Mill	0.0214	1.5481	0.1737	9.80	34.085	10.171	23.914	16.332
21	Lake Greta	0.0110	1.3000	0.1140	8.90	22.581	12.140	10.442	11.441
22	Glen	0.0095	3.9306	0.2077	41.30	55.731	18.358	37.373	24.575
23	Hut	0.4424	2.3297	0.7642	4.40	50.101	18.875	31.226	29.642
24	Lake Pearson	0.0018	0.1954	0.0072	2.36	-	-	-	-
25	Mystery Tarn	0.0058	0.3258	0.0306	0.40	7.202	0.557	6.645	0.386
26	Lake Evelyn	0.0038	0.2259	0.0278	0.60	10.917	6.024	4.893	8.391
27	Lake Heron	0.0002	0.1441	0.0046	0.95	-	-	-	-
28	Lake Camp	0.0064	0.3290	0.0338	0.50	14.058	7.492	6.567	8.495
29	Lake Roundabout	0.0220	0.7061	0.1129	1.20	14.028	4.590	9.438	7.315
30	Lake Emma	0.0090	0.7253	0.0608	2.10	20.686	8.737	11.949	9.406
31	Groynes	0.0043	0.3089	0.0445	2.50	10.818	5.500	5.318	8.322
32	Lake Forsyth	0.0090	2.5000	0.5500	181.00	-	-	-	-
33	Lake Middleton	0.0069	0.4094	0.0100	0.60	10.270	3.049	7.220	3.663
34	Red Lagoon	0.0056	0.5834	0.0372	0.15	11.521	1.987	9.535	3.285
35	Swan Lagoon	0.0030	3.7637	0.0100	1.50	64.716	4.993	59.723	5.127
36	Avon	0.0036	0.5083	0.0481	0.60	13.952	4.312	9.640	6.467
37	Lake Sylvan	0.0043	0.1818	0.0322	0.50	7.771	1.752	6.019	5.334
38	Lake Harris	0.0297	0.1699	0.0100	0.15	3.571	2.275	1.296	2.562
39	Lake Mackenzie	0.0280	0.0100	0.0310	0.15	1.033	0.282	0.750	0.612
40	Gertrude Saddle	0.0322	0.0989	0.0253	0.15	1.284	0.145	1.139	0.133
41	Lake Howden	0.0292	0.1151	0.0100	0.20	14.309	10.087	4.222	22.230
42	Lake Hayes	0.0028	0.2400	0.0100	1.99	-	-	-	-
43	Lake Johnson	0.0067	0.7069	0.0100	0.40	34.450	14.547	19.902	26.443
44	"Sugarbowl Tarn"	0.0049	0.0936	0.0263	0.20	3.971	1.486	2.485	4.126
45	Lake Alta	0.0052	0.0920	0.0246	0.15	2.058	1.139	0.919	1.645
46	Lake Mistletoe	0.0299	0.1494	0.0274	1.10	11.159	6.741	4.417	0.881
	Max	1.9701	6.0750	2.8038	181.00	65.472	19.094	59.723	29.642
	Min	0.0002	0.0100	0.0046	0.15	1.033	0.145	0.750	0.133
	Mean	0.0630	0.7889	0.1335	8.54	18.018	5.846	12.163	8.084
	Median	0.0061	0.3173	0.0292	1.11	10.917	4.300	6.494	5.334
	SD	0.2946	1.2285	0.4286	27.40	19.318	5.469	15.847	8.049

B3: Complete set of lake data part 3. Highlighted head-capsule counts were below the cut-off (50)

Lake nr	Location	Mg (mg/L)	Na (mg/L)	K (mg/L)	Cl (mg/L)	SO_4 (mg/L)	HC Count	# Taxa	Diversity H'
1	Lake Rotorua N	-	-	-	-	-	67	8	0.7138
2	Lake Rotoehu	-	-	-	-	-	114.5	9	0.5935
3	Lake Rerewhakaaitu	-	-	-	-	-	216.5	14	0.7782
4	Lake Okaro	-	-	-	-	-	63	7	0.3465
5	Lake Tutira	-	-	-	-	-	119.5	10	0.7149
6	Lake Dudding	-	-	-	-	-	68	9	0.3419
7	Iron Lake	0.360	1.240	0.100	1.780	0.200	89	6	0.5571
8	Lake Sylvester	0.710	1.310	0.070	1.460	0.200	56.5	9	0.5284
9	Little Sylvester Lake	1.160	1.340	0.030	1.430	0.200	59.5	14	0.8466
10	Rainbow Skifield W	0.150	0.830	0.170	0.360	0.200	337	8	0.4398
11	Rainbow Skifield E	0.150	1.050	0.110	0.190	1.400	111.5	7	0.6479
12	Lake Sedgemere	1.015	2.814	0.600	0.986	0.378	235.5	16	0.6764
13	Princess Bath	0.090	0.630	0.020	0.020	0.500	81	3	0.4259
14	Lake Rotorua S	3.178	20.891	1.965	23.702	0.200	104	13	0.8703
15	Horseshoe Lake	2.181	6.693	1.065	3.098	3.160	331.5	13	0.7506
16	Lake Taylor	-	-	-	-	-	134.5	11	0.4818
17	Lake Mason	-	-	-	-	-	53.5	14	0.9102
18	Lake Sheppard	-	-	-	-	-	51.5	12	0.8122
19	St Annes Lagoon	9.734	43.640	4.362	48.618	11.678	95	7	0.2876
20	Mill	5.631	24.340	1.937	29.748	20.932	76	9	0.5401
21	Lake Greta	5.192	20.709	2.732	14.542	12.176	17	4	0.3656
22	Glen	11.255	41.668	4.741	45.233	35.606	534	14	0.3192
23	Hut	4.323	19.202	5.144	16.923	8.784	70	6	0.2682
24	Lake Pearson	-	-	-	-	-	156	8	0.3710
25	Mystery Tarn	0.139	1.228	0.218	1.637	0.326	425	16	0.9336
26	Lake Evelyn	1.342	3.129	0.258	1.058	3.001	208	12	0.5808
27	Lake Heron	-	-	-	-	-	64	7	0.6855
28	Lake Camp	1.500	3.481	0.393	1.289	0.794	114	12	0.8361
29	Lake Roundabout	2.111	4.267	0.213	2.900	1.128	63.5	8	0.6166
30	Lake Emma	2.242	5.120	0.323	1.674	1.528	131.5	13	0.8061
31	Groynes	1.057	3.321	0.585	2.128	4.857	120	6	0.6641
32	Lake Forsyth	-	-	-	-	-	30	1	0.0000
33	Lake Middleton	0.742	2.240	0.223	1.082	0.581	173.5	8	0.5469
34	Red Lagoon	0.740	3.094	0.171	1.209	0.381	150	21	1.0393
35	Swan Lagoon	1.954	11.841	3.193	6.081	0.200	65	7	0.6181
36	Avon	0.985	3.294	0.157	1.230	1.874	89	12	0.7920
37	Lake Sylvan	0.569	1.516	0.348	1.623	2.254	88	18	0.8736
38	Lake Harris	0.109	0.551	0.077	0.951	0.524	112	19	1.0518
39	Lake Mackenzie	0.059	0.222	0.135	0.778	0.316	156.5	14	0.6510
40	Gertrude Saddle	0.066	0.330	0.035	4.093	0.217	199	19	0.7256
41	Lake Howden	0.333	1.327	0.148	1.336	2.832	255.5	19	0.9308
42	Lake Hayes	-	-	-	-	-	50	12	0.8605
43	Lake Johnson	2.784	5.113	2.300	4.336	7.120	27	7	0.7129
44	"Sugarbowl Tarn"	0.222	0.298	0.139	0.766	2.066	195	5	0.5157
45	Lake Alta	0.133	0.498	0.086	0.811	1.001	72.5	5	0.4320
46	Lake Mistletoe	0.376	0.318	0.097	0.777	0.350	52.5	18	1.0486
	Max	11.255	43.640	5.144	48.618	35.606	534.0	21.0	1.0518
	Min	0.059	0.222	0.020	0.020	0.200	17.0	1.0	0.0000
	Mean	1.897	7.198	0.974	6.783	3.847	132.2	10.7	0.6415
	Median	0.985	2.814	0.218	1.460	1.001	99.5	9.5	0.6576
	SD	2.663	11.309	1.477	12.449	7.294	105.5	4.7	0.2323

B4: Catchment vegetation and land-use data.

Lake nr	Location	Catchment coverage (%)											
		Native forest	Tussock/ herbfield	Tussock/ grassland	Rock/ scree	Snow	Scrub	Pasture	Exotic	Lakes	Swamp	Crops	Populated
1	Lake Rotorua N	0	0	0	0	0	35	50	5	0	0	0	10
2	Lake Rotoehu	0	0	0	0	0	55	35	20	0	0	0	0
3	Lake Rerewhakaaitu	0	0	0	0	0	15	45	35	0	5	0	0
4	Lake Okaro	0	0	0	0	0	10	90	0	0	0	0	0
5	Lake Tutira	0	0	15	0	0	15	50	20	0	0	0	0
6	Lake Dudding	0	0	0	0	0	5	75	20	0	0	0	0
7	Iron Lake	0	40	0	60	0	0	0	0	0	0	0	0
8	Lake Sylvester	10	50	0	40	0	0	0	0	0	0	0	0
9	Little Sylvester Lake	0	50	0	50	0	0	0	0	0	0	0	0
10	Rainbow Skifield W	0	60	0	40	0	0	0	0	0	0	0	0
11	Rainbow Skifield E	0	25	0	70	0	5	0	0	0	0	0	0
12	Lake Sedgemere	0	0	70	0	0	0	0	0	10	20	0	0
13	Princess Bath	0	8	0	90	2	0	0	0	0	0	0	0
14	Lake Rotorua S	0	0	45	0	0	30	20	5	0	0	0	0
15	Horseshoe Lake	10	0	30	0	0	30	20	10	0	0	0	0
16	Lake Taylor	10	0	65	0	0	5	5	0	15	0	0	0
17	Lake Mason	70	0	20	0	0	10	0	0	0	0	0	0
18	Lake Sheppard	5	0	60	0	0	30	0	0	5	0	0	0
19	St Annes Lagoon	0	0	0	0	0	10	75	5	0	0	10	0
20	Mill	0	0	0	0	0	10	80	10	0	0	0	0
21	Lake Greta	0	0	0	0	0	0	95	5	0	0	0	0
22	Glen	0	0	0	0	0	5	90	5	0	0	0	0
23	Hut	0	0	0	0	0	5	90	5	0	0	0	0
24	Lake Pearson	5	0	70	5	0	10	0	5	5	0	0	0
25	Mystery Tarn	5	0	70	10	0	15	0	0	0	0	0	0
26	Lake Evelyn	10	0	45	0	0	40	0	5	0	0	0	0
27	Lake Heron	0	0	65	0	0	5	0	5	0	25	0	0
28	Lake Camp	0	0	75	0	0	20	0	5	0	0	0	0
29	Lake Roundabout	0	0	75	0	0	30	0	0	0	0	0	0
30	Lake Emma	0	0	70	0	0	30	0	0	5	0	0	0
31	Groynes	0	0	0	0	0	0	70	25	0	0	0	0
32	Lake Forsyth	5	0	50	0	0	15	30	0	0	0	0	0
33	Lake Middleton	0	0	35	0	0	20	0	45	0	0	0	0
34	Red Lagoon	0	0	85	0	0	10	0	5	0	0	0	0
35	Swan Lagoon	0	0	95	0	0	0	0	5	0	0	0	0
36	Avon	0	0	45	5	0	20	30	0	0	0	0	0
37	Lake Sylvan	90	10	0	0	0	0	0	0	0	0	0	0
38	Lake Harris	0	30	0	45	10	10	0	0	5	0	0	0
39	Lake Mackenzie	20	30	0	20	5	25	0	0	0	0	0	0
40	Gertrude Saddle	0	10	0	80	10	0	0	0	0	0	0	0
41	Lake Howden	30	20	0	30	5	15	0	0	0	0	0	0
42	Lake Hayes	0	0	55	0	0	15	20	5	0	0	0	5
43	Lake Johnson	0	0	55	0	0	20	15	10	0	0	0	0
44	"Sugarbowl Tarn"	0	10	0	90	0	0	0	0	0	0	0	0
45	Lake Alta	0	20	0	76	4	0	0	0	0	0	0	0
46	Lake Mistletoe	30	0	20	0	0	40	0	0	0	10	0	0
	Max	90	60	95	90	10	55	95	45	15	25	10	10
	Min	0	0	0	0	0	0	0	0	0	0	0	0
	Mean	6.52	7.89	26.41	15.46	0.78	13.37	21.41	5.65	0.98	1.30	0.22	0.33
	SD	17.48	15.58	31.56	27.91	2.32	13.46	32.07	9.70	2.91	4.88	1.47	1.63

APPENDIX C: SUPPLEMENTARY TABLES FROM NUMERICAL ANALYSES

Altitude	1												
Area	-0.3962	1											
Feb Mean	-0.9445	0.4773	1										
Cond	-0.747	0.3002	0.7133	1									
pH	-0.2645	-0.0117	0.276	0.3314	1								
Depth	0.1278	0.4382	-0.1707	-0.1968	-0.2817	1							
NOx-N	0.0893	-0.353	-0.0169	0.014	0.0953	-0.183	1						
React P	-0.184	-0.2624	0.1023	0.285	0.1461	-0.3613	0.162	1					
TN	-0.6157	0.1183	0.6725	0.6485	0.4659	-0.5431	0.1027	0.3435	1				
TP	-0.3484	-0.1658	0.3255	0.4862	0.4342	-0.5266	0.2576	0.6707	0.5889	1			
Chla	-0.6527	0.4772	0.742	0.682	0.313	-0.1183	0.013	0.126	0.6468	0.4072	1		
Lat	0.1909	-0.4365	-0.4035	-0.2026	0.0748	-0.0841	-0.2702	0.0795	-0.1351	-0.035	-0.5687	1	
Long	-0.3197	0.3838	0.5283	0.3066	0.0468	-0.014	0.3142	-0.082	0.3062	0.1603	0.6879	-0.9468	1
Native	-0.1621	0.0633	-0.0294	-0.0774	-0.2042	0.2837	-0.2886	-0.0829	-0.3445	-0.2041	-0.2219	0.25	-0.3162
Tuss._he	0.7509	-0.3399	-0.7706	-0.5353	-0.182	0.2476	0.2568	-0.0318	-0.654	-0.2139	-0.5441	0.0736	-0.258
Tuss._gr	-0.2396	0.2105	0.2397	0.0053	0.0749	-0.1251	-0.3548	-0.2454	0.2633	-0.1459	-0.0521	0.3036	-0.18
Rock	0.8974	-0.4884	-0.8975	-0.5753	-0.2133	0.129	0.1968	-0.0414	-0.6073	-0.2309	-0.5649	0.1755	-0.3123
Scrub	-0.5419	0.439	0.5352	0.3467	0.1714	-0.0457	-0.2482	0.2004	0.2446	0.1744	0.3193	-0.1401	0.1558
Past.	-0.6282	0.1446	0.7081	0.6845	0.2415	-0.1281	0.2441	0.2664	0.56	0.463	0.7231	-0.4987	0.6034
Exotic	-0.5695	0.2854	0.6677	0.373	0.1402	-0.152	0.165	-0.0892	0.4033	0.0349	0.4469	-0.3218	0.4198
Lake	0.0457	0.2094	-0.0722	-0.1458	-0.0242	0.1589	-0.38	0.0348	-0.0288	-0.1748	0.023	0.0638	-0.0237
Swamp	-0.0403	0.1732	0.0268	-0.1218	-0.1357	0.0841	0.0135	-0.1574	-0.0571	-0.1717	-0.0459	-0.0014	-0.0013
Popul.	-0.1734	0.4943	0.2382	0.284	0.0184	0.1903	-0.4572	0.0486	0.0614	0.0195	0.2923	-0.2019	0.1254
Richness	-0.1395	-0.0636	-0.0415	-0.0124	-0.104	-0.0007	-0.2716	0.2177	-0.0506	-0.0119	-0.3104	0.2932	-0.3858
H.	-0.1067	0.1138	-0.0208	-0.11	-0.0435	0.1017	-0.3534	-0.0873	-0.1418	-0.1703	-0.3463	0.2659	-0.356
	Altitude	**Area**	**Feb Mean**	**Cond**	**pH**	**Depth**	**NOx-N**	**React P**	**TN**	**TP**	**Chla**	**Lat**	**Long**

Table C1: Correlation matrix of catchment characteristics and limnological variables from the entire training set

	1												
Tuss._he	0.0791	1											
Tuss._gr	-0.0041	-0.569	1										
Rock	-0.1172	0.8226	-0.5049	1									
Scrub	0.1021	-0.5134	0.3464	-0.541	-0.149	1							
Past.	-0.3099	-0.4323	-0.328	-0.4433	-0.2717	0.1645	1						
Exotic	-0.3013	-0.4901	0.0165	-0.5115	-0.308	0.2619	0.5322	1					
Lake	0.0235	-0.1254	0.3716	-0.122	0.0478	0.0033	-0.2126	-0.2442	1				
Swamp	-0.0118	-0.1938	0.2217	-0.2096	-0.1218	-0.0367	-0.1258	0.0274	0.1838	1			
Popul.	-0.1182	-0.1376	-0.0226	-0.1488	-0.0865	0.2113	0.2226	0.0891	-0.087	-0.0683	1		
Richness	0.3719	0.0241	0.1338	-0.0862	0.3916	0.2043	-0.229	-0.1967	0.1858	0.1091	-0.0799	1	
H.	0.3234	-0.0295	0.3076	-0.1081	0.148	0.3232	-0.3622	-0.1507	0.0117	0.1566	0.1119	0.725	1
	Native	**Tuss._he**	**Tuss._gr**	**Rock**	**Snow**	**Scrub**	**Past.**	**Exotic**	**Lake**	**Swamp**	**Popul.**	**Richness**	**H.**

Table C2: Correlation matrix of catchment characteristics and limnological variables from the entire training set

Table C3: Interset correlation matrix from a RDA of the catchment and limnological data.

INTERSET CORRELATION MATRIX: All sites included in the analysis

SPEC AX1	1							
SPEC AX2	0	1						
SPEC AX3	0	0	1					
SPEC AX4	0	0	0	1				
ENVI AX1	1	0	0	0	1			
ENVI AX2	0	1	0	0	0	1		
ENVI AX3	0	0	1	0	0	0	1	
ENVI AX4	0	0	0	1	0	0	0	1
Altitude	0.864	0.302	0.132	-0.135	0.864	0.302	0.132	-0.135
Area	-0.456	-0.415	0.583	0.224	-0.456	-0.415	0.583	0.224
Feb Mean	-0.951	-0.169	0.029	0.035	-0.951	-0.169	0.029	0.035
Cond	-0.776	0.021	-0.203	0.274	-0.776	0.021	-0.203	0.274
pH	-0.373	0.117	-0.372	-0.130	-0.373	0.117	-0.372	-0.130
Depth	0.271	-0.252	0.628	0.369	0.271	-0.252	0.628	0.369
NOx-N	-0.038	0.708	-0.082	-0.184	-0.038	0.708	-0.082	-0.184
React P	-0.175	0.224	-0.656	0.406	-0.175	0.224	-0.656	0.406
TN	-0.779	0.083	-0.402	-0.180	-0.779	0.083	-0.402	-0.180
TP	-0.468	0.347	-0.619	0.144	-0.468	0.347	-0.619	0.144
Chla	-0.857	0.173	0.173	0.116	-0.857	0.173	0.173	0.116
Lat	0.470	-0.370	-0.598	-0.165	0.470	-0.370	-0.598	-0.165
Long	-0.619	0.391	0.512	0.004	-0.619	0.391	0.512	0.004
Native	0.215	-0.486	-0.021	0.279	0.215	-0.486	-0.021	0.279
Tuss._he	0.769	0.390	0.095	0.257	0.769	0.390	0.095	0.257
Tuss._gr	-0.183	-0.676	-0.098	-0.578	-0.183	-0.676	-0.098	-0.578
Rock	0.824	0.451	0.028	0.134	0.824	0.451	0.028	0.134
Snow	0.580	0.010	-0.204	0.507	0.580	0.010	-0.204	0.507
Scrub	-0.502	-0.455	-0.090	0.225	-0.502	-0.455	-0.090	0.225
Past.	-0.768	0.396	0.019	0.257	-0.768	0.396	0.019	0.257
Exotic	-0.640	0.087	0.174	-0.107	-0.640	0.087	0.174	-0.107
Lake	0.066	-0.383	0.085	-0.182	0.066	-0.383	0.085	-0.182
Swamp	-0.006	-0.283	0.180	-0.338	-0.006	-0.283	0.180	-0.338
Popul.	-0.271	-0.175	0.267	0.464	-0.271	-0.175	0.267	0.464
Richness	0.179	-0.556	-0.412	0.344	0.179	-0.556	-0.412	0.344
H.	0.168	-0.688	-0.188	0.205	0.168	-0.688	-0.188	0.205
	SPEC AX1	**SPEC AX2**	**SPEC AX3**	**SPEC AX4**	**ENVI AX1**	**ENVI AX2**	**ENVI AX3**	**ENVI AX4**

Axes		1	2	3	4	Total inertia
Eigenvalues	:	0.323	0.156	0.07	0.042	1.349
Lengths of gradient	:	**2.336**	1.971	1.502	1.375	
Cumulative percentage variance of species data	:	23.9	35.5	40.7	43.7	
Sum of all eigenvalues						1.349

Table C4: Results of a DCA of the speies data from the "ion dataset". 2% deletion criteria.

name	(weighted) mean	stand. dev.	inflation factor
SPEC AX1	0	1.0289	
SPEC AX2	0	1.0898	
SPEC AX3	0	1.0473	
SPEC AX4	0	1.095	
ENVI AX1	0	1	
ENVI AX2	0	1	
ENVI AX3	0	1	
ENVI AX4	0	1	
Feb Mean	13.29	2.7014	5.5898
IOC	0.513	0.4841	12.6873
OC	0.7601	0.5001	25.5881
Ca	0.6195	0.5277	9.9799
Mg	-0.1537	0.5939	22.0355
Na	0.3651	0.5993	24.6521
K	-0.5686	0.605	7.1243
Cl	0.2733	0.6195	5.616
SO4	-0.0071	0.6136	4.2744
NOx-N	-2.1563	0.3296	1.8227
React P	-1.9684	0.5793	3.6371
TN	-0.5231	0.6046	16.5379
TP	-1.4265	0.5353	5.4457
Chla	-0.1139	0.589	4.0147

Table C5: Variance inflation factors (VIFs) for the 15 limnological variables from the "ion dataset". Conductivity (Cond) and TC were removed prior to the initial CCA.

Table C6: Results of a series of partial CCAs for the 7 significant environmental variables from the ion dataset.

Variable	Co-variable	λ_1/λ_2	P	cum%
Feb Mean	None	0.706	0.001	15..1
	IOC	0.326	0.022	8
	K	0.418	0.007	8.8
	SO4	0.570	0.001	12.6
	TN	0.775	0.001	9.2
	Chla	0.556	0.003	11.9
IOC	None	0.419	0.006	9.40
	Feb mean	0.132	0.484	3.3
	K	0.185	0.245	4.1
	SO4	0.235	0.172	5.1
	TN	0.139	0.556	3.4
	Chla	0.248	0.172	5.4
K	None	0.817	0.001	15.90
	Feb mean	0.464	0.003	9.7
	IOC	0.484	0.002	10.6
	SO4	0.303	0.41	6.9
	TN	0.304	0.042	6.9
	Chla	0.370	0.04	7.6
SO4	None	0.464	0.002	9.30
	Feb mean	0.295	0.022	6.9
	IOC	0.264	0.089	6.1
	K	0.080	0.921	2
	TN	0.269	0.065	6.1
	Chla	0.296	0.048	6.7
Ca	None	0.666666667	0.001	10.70
	Feb mean	0.238	0.308	4.5
	K	0.183	0.651	3.4
	SO4	0.388	0.034	6.9
	TN	0.285	0.147	5.2
	Chla	0.291	0.162	5.2
TN	None	0.696	0.001	13.60
	IOC	0.255	0.11	6
	K	0.183	0.26	4.2
	SO4	0.355	0.024	8.3
	Chla	0.270	0.087	6.1
Chla	None	0.571	0.001	11.40
	Feb mean	0.281	0.056	6.2
	K	0.163	0.383	3.8
	SO4	0.296	0.038	6.7
	TN	0.178	0.369	4.2
	IOC	0.234	0.2	5.5

APPENDIX D: PEER REVIEWED JOURNAL ARTICLES THAT HAVE BEEN PUBLISHED OR THAT ARE IN PRESS

Note regarding published and in press papers

As a requirement of the University of Canterbury PhD thesis regulations I would like to clarify the nature of my contribution the journal articles included in this appendix.

My main supervisor (Dr Jamie Shulmeister) is listed as second author on all three papers included in this appendix. I was responsible for the collection of data, its interpretation and the drafting of the initial manuscript for all three papers. As my PhD supervisor Dr Shumeister assisted me with the interpretation and provided criticism of drafts of these papers.

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A Holocene record of human induced and natural environmental change from Lake Forsyth (Te Wairewa), New Zealand

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Abstract

A 1.2 m sediment core from Lake Forsyth, Canterbury, New Zealand, records the development of the catchment/lake system over the last 7000 years, and its response to anthropogenic disturbance following European settlement c. 1840 AD. Pollen was used to reconstruct catchment vegetation history, while foraminifera, chironomids, Trichoptera, and the abundance of *Pediastrum simplex* colonies were used to infer past environmental conditions within the lake. The basal 30 cm of core records the transition of the Lake Forsyth Basin from a tidal embayment to a brackish coastal lake. Timing of closure of the lake mouth could not be accurately determined, but it appears that Lake Forsyth had stabilised as a slightly brackish, oligo-mesotrophic shallow lake by about 500 years BP. Major deforestation occurred on Banks Peninsula between 1860 AD and 1890 AD. This deforestation is marked by the rapid decline in the main canopy trees (*Prumnopitys taxifolia* (matai) and *Podocarpus totara/hallii* (totara/mountain totara), an increase in charcoal, and the appearance of grasses. At around 1895 AD, pine appears in the record while a willow (*Salix* spp.) appears somewhat later. Redundancy analysis (RDA) of the pollen and aquatic species data revealed a significant relationship between regional vegetation and the abundance of aquatic taxa, with the percentage if disturbance pollen explaining most (14.8%) of the constrained variation in the aquatic species data. Principle components analysis (PCA) of aquatic species data revealed that the most significant period of rapid biological change in the lakes history corresponded to the main period of human disturbance in the catchment. Deforestation led to increased sediment and nutrient input into the lake which was accompanied by a major reduction in salinity. These changes are inferred from the appearance and proliferation of freshwater algae (*Pediastrum simplex*), an increase in abundance and diversity of chironomids, and the abundance of cases and remains from the larvae of the caddisfly, *Oecetis unicolor*. Eutrophication accompanied by increasing salinity of the lake is inferred from a significant peak and then decline of *P. simplex*, and a reduction in the abundance and diversity of aquatic invertebrates. The artificial opening of the lake to the Pacific Ocean, which began in the late 1800s, is the likely cause of the recent increase in salinity. An increase in salinity may have also encouraged blooms of the halotolerant and hepatotoxic cyanobacteria *Nodularia spumigena*.

Introduction

Coastal waterways are under pressure from the effects of development and over-population worldwide, and are the subject of increasing human intervention for management purposes (UNESCO 2003). Management of these aquatic ecosystems frequently focuses on two outcomes;

either the maintenance of a water body in its natural state, or if the water body is significantly degraded, the restoration of the system to a pre-impact state. Determining the original state of a system is not a simple task. Long-term monitoring can be used to characterize a water body and to determine the natural and human induced factors affecting the system. In New Zealand, however, rigorous scientific monitoring of lakes and estuaries only extends back as far the early 1980s (Taylor and Smith 1997) and there are few continuous records of physiochemical parameters. Historical records provide a more long-term record, but do not extend before about 1850 AD, in most places, and are descriptive but not diagnostic. It is generally agreed that most impacts on waterways in New Zealand have occurred since European arrival about 200 years ago (Taylor and Smith 1997) but these impacts are neither quantified, nor in many cases, even certain to have occurred.

This paper presents a multiproxy study of a record from Lake Forsyth (Te Wairewa), Banks Peninsula, Canterbury, New Zealand (Figure 1). There is historical literature referring to this lake and its catchment extending back to the late 1830s (Petrie 1963; Soons 1998), while lake monitoring data consists of an almost continuous record from 1993 (Canterbury Regional Council, unpublished data). The primary aim of this project is to provide guidance for the future management of Lake Forsyth and its catchment by providing information on natural and human-induced changes in the lake/catchment system in the past. Many restoration based paleolimnological studies assume slow or no natural change in the aquatic ecosystem being examined. In the case of Lake Forsyth, however, recent environmental changes are the result of both rapid coastal evolution (a 'natural' phenomenon) and human disturbance. This paper provides a case study in the use of a multiproxy paleobiological approach to distinguish between human impacts and the development of a near coastal waterway system. This investigation involves the first use of Trichoptera (caddisflies), and is one of only a few studies to use chironomids in paleoecological studies in New Zealand (see Deevy 1955; Boubee 1983; Schakau 1986, 1991, 1993).

While chironomids have now been used extensively in the Northern Hemisphere (e.g., Brooks et al. 1997; Quinlan and Smol 2002; Brooks and Birks 2004) Trichoptera have only been used in a few paleoenvironmental studies (e.g., Ponel et al. 1999; Solem and Birks 2000; Greenwood et al. 2003). The larvae of modern Trichoptera species are common in many lentic and lotic habitats (Greenwood et al. 2003). Like the Chironomidae, information on the ecology and distribution of modern Trichoptera larvae can be used to derive paleoenvironmental information from fossil species. Trichoptera larvae are usually represented by the chitinous sclerites, mandibles (Figure 3b), appendages (Figure 3c) and the remains of cases constructed from sand grains or organic detritus (Figure 3a). In this study the Trichoptera are represented by a single species, *Oecetis unicolor* McLachlan. However, the ecology and distribution of this species is well documented (e.g., Stark 1981; Timms 1982, 1983) and even the addition of one species provides useful information, especially considering the low diversity of chironomid fauna in this record. It is quite likely that invertebrate assemblages derived from brackish water bodies (such as Lake Forsyth) will yield low chironomid diversities, making it necessary to compliment the chironomid record with other proxies.

The study site

Lake Forsyth (Te Wairewa) (43°48 S, 172°44 E, 20 m above mean sea level (amsl)) is a shallow (<4 m deep), hypertrophic, slightly brackish lake situated on the southern side of Banks Peninsula, on the east coast of the South Island, New Zealand (Figure 1). The lake is isolated from the Pacific Ocean by a narrow (≤ 100 m) gravel barrier that is an extension of the Kaitorete "Spit". Kaitorete "Spit" extends some 30 km from Taumutu in the south to the flanks of Banks Peninsula in the north.

The present configuration of Kaitorete "Spit" (more accurately described as a relict spit and active barrier beach complex) has evolved over a period of $\sim$8000 years as a result of the accumulation of material transported north along the Canterbury Bight by long shore currents (Soons et al. 1997).

Historical accounts state that cargo vessels navigated the channel connecting Lake Forsyth to the ocean until the late 1830s, however it was possible to walk across the barrier by 1843 (Soons 1998). The lake normally drains by percolating

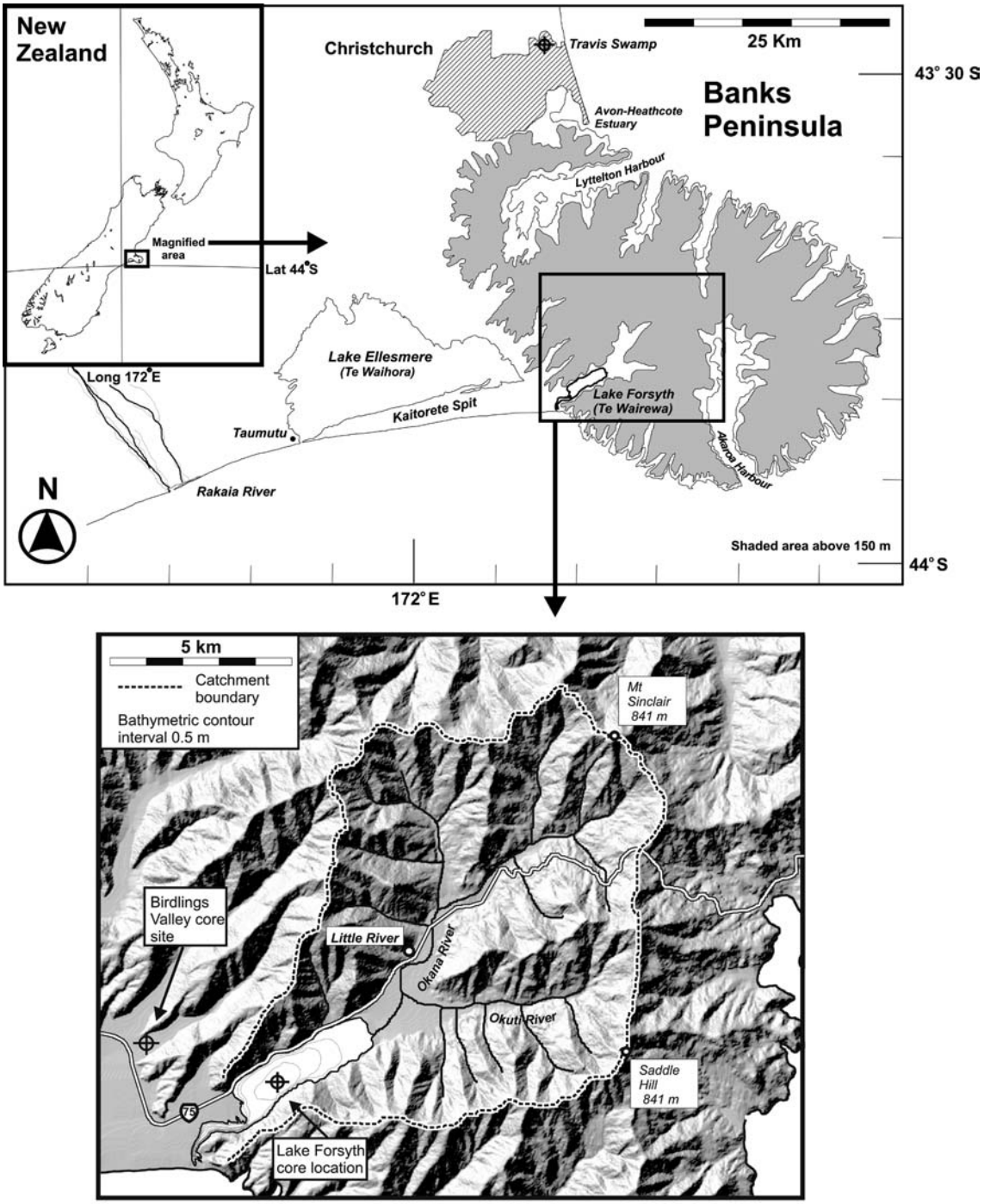

Figure 1. The location of Lake Forsyth, South Island, New Zealand. Two other sites mentioned in the text; Travis Swamp (McGlone 1995, cited in McGlone and Wilmshurst 1999 and Birdlings Valley (Soons et al. 1997) are also shown.

through the gravels of the barrier. However, the lake is artificially opened when lake levels are high to prevent the flooding of local roads and farms. The gravel barrier was first artificially opened in 1866, and is currently opened about once every year, depending on rainfall (Main 2002).

The Lake Forsyth catchment covers approximately 110 km^2 ranging from about sea level to 840 m (amsl) (Figure 1). Most of the catchment was covered in broadleaf/podocarp forest until ~1895, by which time most of the trees had been removed for timber, or burnt in fires that were either deliberate or accidental (Petrie 1963). Since deforestation, most of the catchment has been used for pastoral agriculture. After 1907 the lake became prone to regular blooms of the hepatotoxic cyanobacteria *Nodularia spumigena* Mertens, which have been associated with the appearance of large numbers of dead fish (Main 2002). There is currently a significant long-fin eel (*Anguilla dieffenbachia* Gray), population in the lake, but Maori oral tradition recalls a more diverse and abundant fish fauna in the past (Main 2002).

Materials and methods

Coring

A percussion corer was used to obtain a 1.2 m sediment core (FORS1- LC) from the deepest point of the main depositional basin (Figure 1). The top 10 cm of this core collapsed due to a high water content. A short (50 cm) gravity core was recovered from the same location to allow sampling of this part of the sequence. The sharp transition from light grey gyttja to dark green aqueous material at ~10 cm (Figures 2 and 4) was the basis for correlation between these two cores.

The main core was divided into two sections. One half was archived in a cool store, while the remaining half was sub-sampled at 1 cm intervals. The gravity core was extruded and sub-sampled on site at 1 cm intervals. The sub-samples were bagged and stored for subsequent processing for palynomorphs and macroinvertebrates.

Chronology

A single sample was recovered at 108–110 cm for AMS radiocarbon dating. The sample comprised organic lake mud, which was dried in an oven for three days at 57 °C, ground and homogenized. 5 g of the resulting powder was sent to the Rafter Radiocarbon Laboratory, Lower Hutt, New Zealand for AMS dating.

Pollen and charcoal analysis

Pollen slides were prepared for analysis following the standard methods outlined in Moore et al. (1991). Two *Lycopodium* tablets (Department of Quaternary Geology, Lund University, Sweden. Batch no. 124961) were added to each sample to facilitate the calculation of pollen concentrations (Stockmar 1971). Palynomorphs were identified and counted under a transmitting light microscope with the aid of publications by Pocknall (1981); Large and Braggins (1991); Moore et al. (1991), and Moar (1993). Podocarp pollen was frequently encountered in the form of damaged grains consisting of a corpus with only one sacchus attached, or as an individual sacchi or corpi. In these cases the grains were counted as half grains. The pollen slides were also analysed for charcoal content using the Clark (1982) point count estimation method.

Invertebrate paleontology

Sediment samples were processed for invertebrates following a modified version of the chironomid processing method outlined in Hofmann (1986). It was discovered that this method was also successful in extracting the remains of Trichoptera (caddisfly larvae and cases), molluscs, and foraminifera. Samples were deflocculated in hot 10% KOH and washed through a 93 μm mesh with copious amounts of distilled water. Initial trials with samples from this locality revealed that a quantity of sediment remained inside chironomid headcapsules, obscuring much of the detail required for identification. This problem was resolved by heating the resulting sediment residue in a 10% solution of Calgon®. Samples were then transferred to a Bogorov counting tray and examined for invertebrate remains under a dissection microscope, at 50× magnification.

A preliminary examination of sediment samples from the FORS1-LC core revealed a low chironomid species diversity. Heiri and Lotter (2001) and Quinlan and Smol (2001), have shown that a sample size of 45–50 head capsules is a representative sample of chironomid communities where diversity is low. Sufficient sediment was processed in order to obtain this minimum head capsule abundance. An average of 10 ml of wet sediment

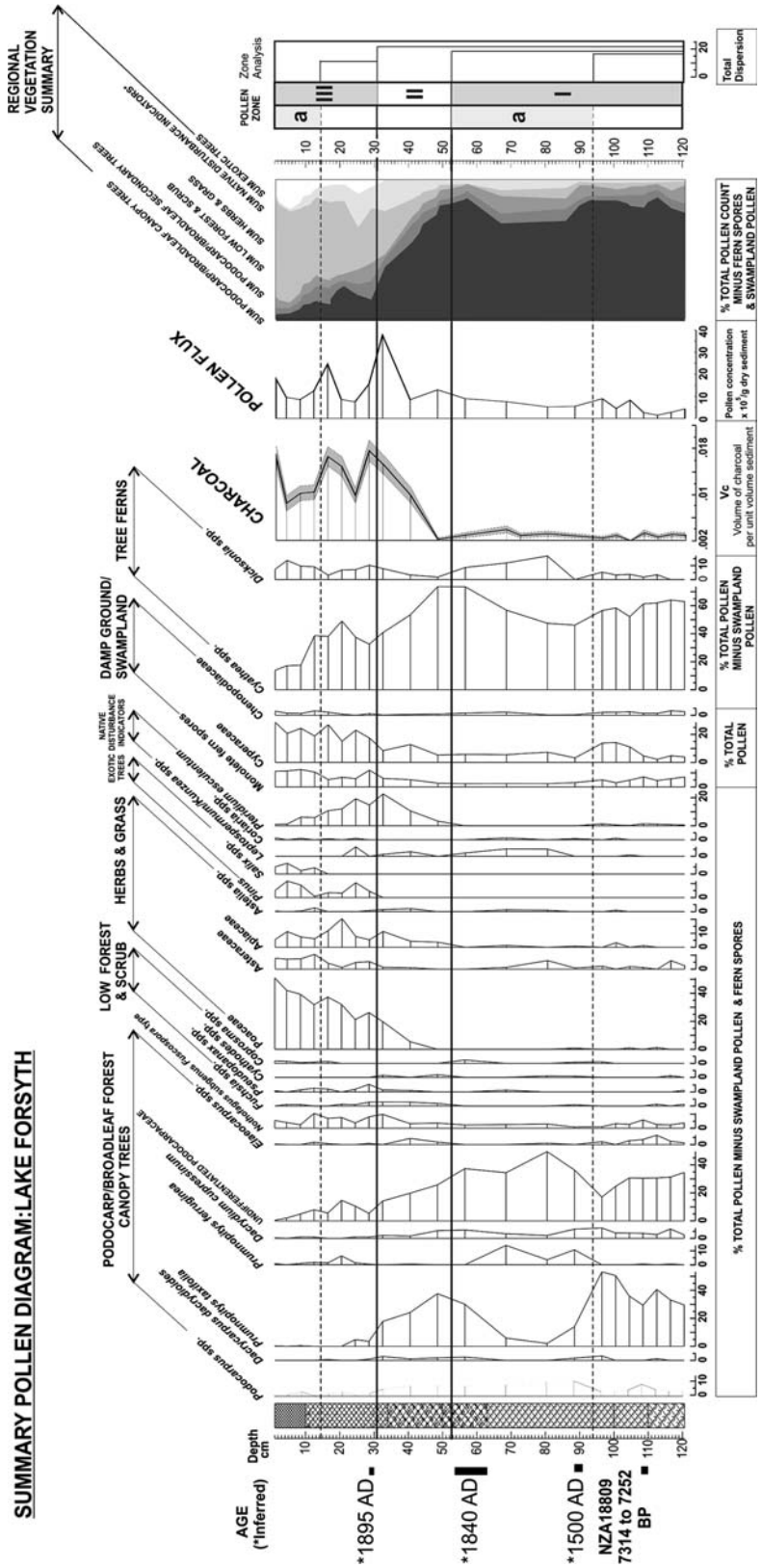

Figure 2. Summary pollen diagram for the Lake Forsyth core.

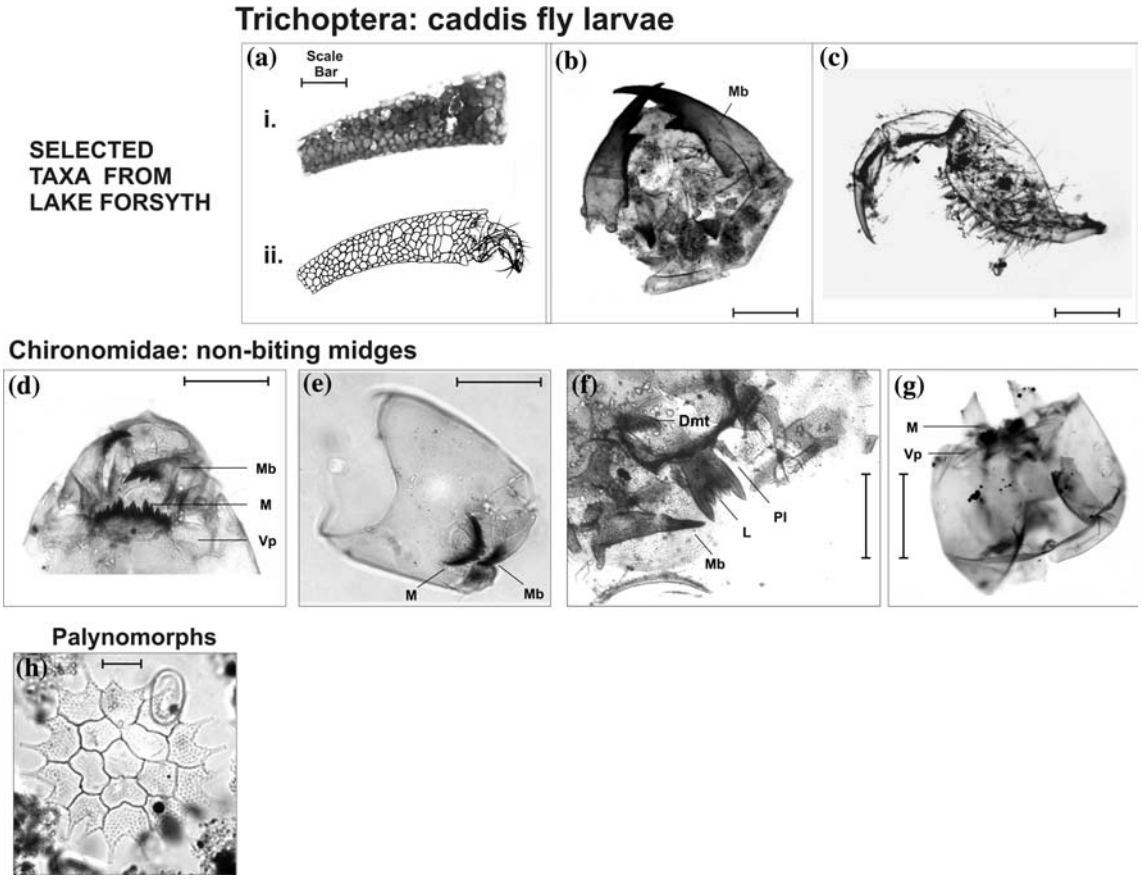

Figure 3. Selected taxa from the Lake Forsyth core. Scale bars are as follows: a: 1 mm; b, c, d, e, and h: 250 μm; f: 125 μm; h: 20 μm. a (i) *Oecetis unicolor* case; a (ii) Reconstruction of *O. unicolor* larvae in case (after Cowley 1978); b and c: Remains of *O. unicolor* larvae; d. *Chironomus* spp.; e. *Crictocopus* spp.; f. Tanypodinae; g. *Corynocera*; h. *Pediastrum simplex*. Abbreviations: Dmt. Dorsomental teeth; L. Ligula; M. Mentum; Mb. Mandible; Pl. Paraligula; Vp. Ventromental plate.

was required to achieve the target head capsule quantity. A corresponding 2 ml sample from each horizon was dried at 50 °C for 3 days and weighed, to enable the calculation of headcapsule concentration per dry weight of sediment.

Insect remains (chironomids, Trichoptera, etc.) were mounted on glass slides in a drop of polyvinyl lactophenol and covered with a glass coverslip. Chironomid head capsules were mounted ventral side up to facilitate identification. Trichoptera larval cases were transferred to a vial of ethanol for preservation to prevent distortion by slide mounting. Foraminifera were mounted on cardboard slides using a tragacanth gum.

Chironomids and Trichoptera were identified using a transmission light microscope with the aid of publications by Boubee (1983); Forsyth (1971), Shakau (1993) and Winterbourn et al. (2000). Foraminifera were identified under a dissecting microscope with the aid of Hayward (1999).

Numerical analysis and display of data

Zonation of pollen and aquatic faunal stratigraphy

The results of the pollen analysis and invertebrate paleontology were plotted using Psimpoll 3.10 (Bennett 2002). Pollen data were displayed as percentage data with a corresponding pollen concentration (Figure 2), while the abundance of chironomids, forams, caddis cases and *Pediastrum simplex* Meyen colonies were plotted as concentrations per gram of dry sediment (Figure 4).

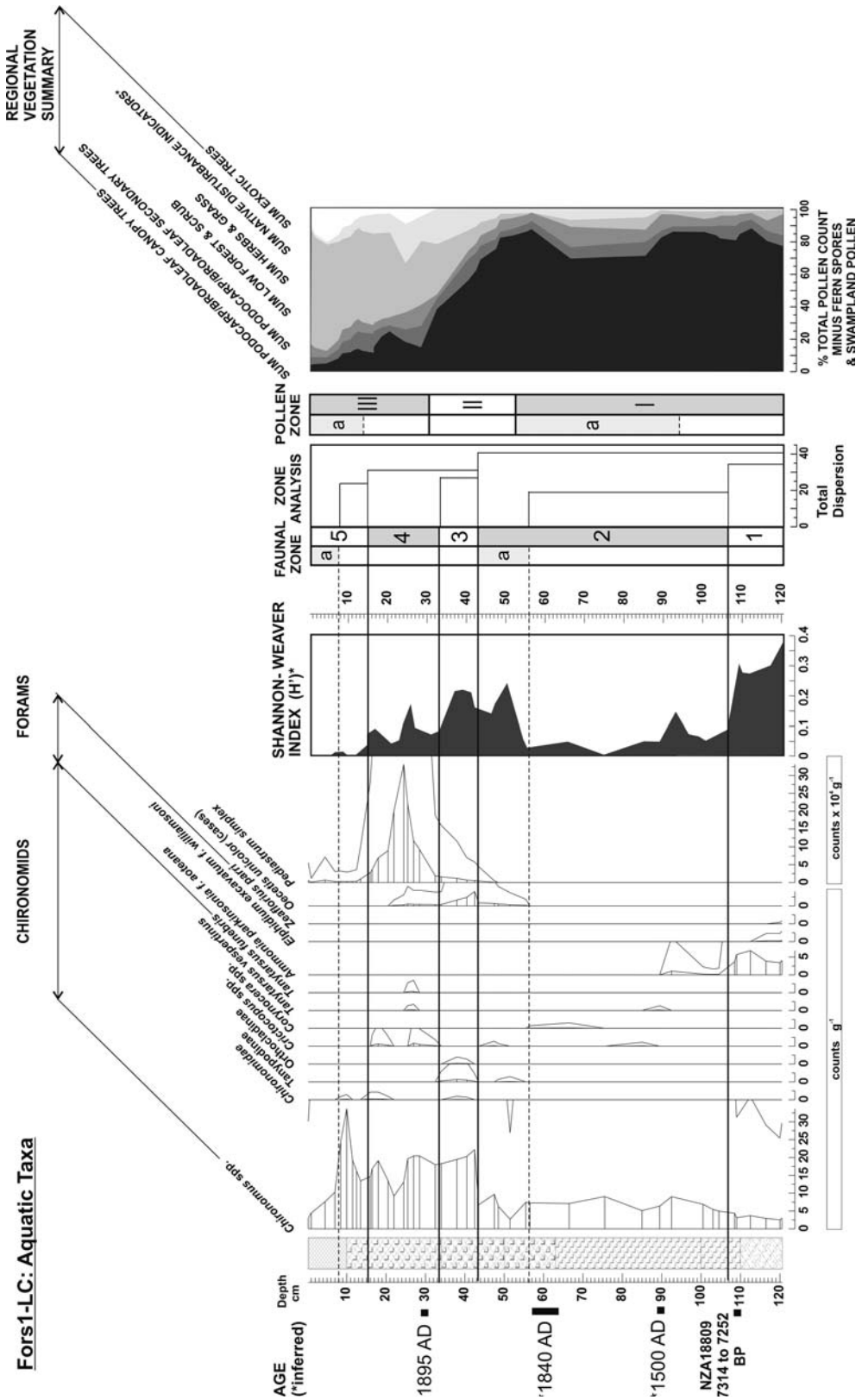

Figure 4. Summary diagram of water quality proxies from the Lake Forsyth core. Pollen zones and a regional vegetation summary are provided for the sake of comparison.
*Shannon Weaver Index (H') = $-\Sigma$ Pi ln Pi, where Pi represents the proportion of the *i*th taxon in the sample (Begon et al. 1986).

The Shannon Weaver Index (H') was used as a measure of the diversity of the aquatic faunal species assemblage. H' was calculated using the equation: $H' = -\sum P_i \ln P_i$, where P_i represents the proportion of the ith taxon in the sample (Begon et al. 1986).

Calculations were based on the concentrations (per gram of dry sediment) of chironomids, trichoptera, and foraminifera present in each sample. The resulting curve of diversity with respect to depth is included in Figure 4.

The CONISS function in Zone 1.2 (Juggins 1992) was used to determine the location of the zone boundaries. The analysis was based on the percentage and concentration data standardized to a mean of zero and to unit standard deviation (Grimm 1987). Separate zone analyses were run on pollen percentage data and concentration data for the aquatic fauna (chironomids, forams, trichoptera, and *P. simplex*) so that zonation in each record distinguished between changes in catchment vegetation and changes in lake taxa.

Podocarp pollen found between 55 and 90 cm was poorly preserved and consequently a large proportion was classified as undifferentiated podocarp pollen. This zone of poor preservation was identified as a zone by the zone analysis. The percentage data for the podocarp pollen was combined for the sake of the zone analysis, to remove the effect of the preservation bias.

Exploratory analysis of aquatic faunal stratigraphy

Exploratory data analysis of the concentration data for the aquatic taxa was performed using CANOCO 4.5 and displayed using Canodraw (ter Braak and Šmilauer 2002). Stratigraphic trends in the species concentration data were investigated using principal components analysis (PCA), as an initial detrended correspondence analysis (DCA) of the log-transformed data revealed that gradient lengths were less than 2 standard deviations (Jongman et al. 1987). The PCA ordination was performed on centred and standardized species data with a focus on inter-sample distances, to reduce the effects of taxa with high concentrations (e.g., *P. simplex*). The samples were connected as a time-track to show the changes in species composition with respect to stratigraphic depth.

Determining the relationship between regional vegetation and aquatic fauna

Redundancy analysis (RDA) was used to explore the relationship between aquatic taxa and regional vegetation. The RDA was performed in CANOCO 4.5 (ter Braak and Šmilauer 2002) using aquatic taxa concentrations (units g^{-1} of dry sediment) for the species data and pollen percentages as environmental data. Pollen percentages for each taxon were assigned to the 6 main vegetation classes listed in the regional vegetation summary in Figures 2 and 4 (Podocarp/Broadleaf Canopy Trees, Podocarp/Broadleaf Secondary Trees, Low Forest and Scrub, Herbs and Grass, Native Disturbance Indicators, and Exotic Trees). Pollen percentages for all taxa belonging to a particular class were combined to give 6 totals, one for each pollen class. It was assumed that the use of combined pollen percentages would provide a clearer indication of regional vegetation trends and reduce the effect of the many species in the record that were present in low concentrations. Examples of the main species belonging to each class are depicted in Figure 2, except for Podocarp/Broadleaf Secondary trees. Abundance curves for pollen from these smaller trees and shrubs that are typical of podocarp/broadleaf forest (e.g. *Shefflera digitata* Forster, *Pittosporum* spp. Hook and *Myrsine* spp. Linnaeus) were omitted from the summary diagram for the sake of clarity, as none of the individual species abundances exceeded 5%.

The redundancy analysis was performed on abundance data taken from above the disappearance of the last salt-tolerant foram species from the record (*Ammonia parkinsonia f. aoteana* Finlay) at about 90 cm depth. This change in aquatic species composition was accompanied by changes in sedimentology, but there was a lack of any major corresponding signal in the pollen record (Figures2 and 4). It was therefore assumed that these changes in the aquatic fauna were the result of the formation of a barrier isolating the Lake Forsyth Basin from the ocean, not changes in regional vegetation. Consequently data for the basal 30 cm of the core was omitted from the analysis to avoid interference with the vegetation/aquatic species correlation. The aquatic invertebrate record was based on a higher sample resolution than the pollen stratigraphy. In performing the numerical analysis, samples from the inverte-

brate record were only used if they had stratigraphic equivalents in the pollen record.

Results

Stratigraphy and chronology

The 1.2 m sediment core (FORS1-LC) was divided into six units (Figures 2 and 4) using the Troels-Smith system (Troels-Smith 1955). The basal 10 cm consisted of a dark grey sandy unit containing abundant large (≤ 2 cm) shell fragments, valves, and one set of attached valves, mainly from *Chione (Austrovenus) stutchburyi* Wood. The shell fragments were more concentrated at the top of the sandy unit. The basal unit was overlain by a 10 cm thick light brown sandy clay horizon; an AMS radiocarbon date from this horizon (108–110 cm) provided an uncalibrated date of 6355 ± 40 BP (NZA 18809). This radiocarbon date was calibrated using INTCAL98 (Stuiver et al. 1998) and yielded an age range of 7331–7211 years BP at 2σ.

The proportion of sand gradually decreased to the top of the sandy clay horizon at 100 cm depth. The sandy clay horizon was overlain by $\sim$35 cm of light brown silty clay. At 63 cm depth, a 30 cm thick layer was differentiated on the basis of an increasing proportion of herb detritus. The top 30 cm of the core was characterized by a rapid increase in the clay content, with the sediment becoming more aqueous and organic rich. The top 10 cm consisted of a dark green aqueous layer which comprised highly humified organic matter.

Pollen and charcoal analysis

The pollen assemblage was dominated by spores from the tree fern *Cyathea* spp. Smith, which contributed up to 73% of the non-swamp pollen total (Figure 2). *Cyathea* spp. spores were usually poorly preserved and showed signs of physical damage or chemical corrosion. The relative abundances for the remaining 150 species found in the record were expressed as percentages, based on the non-swamp (n. sw.) total, and non-swamp total minus tree fern spores (non-swamp/non-spore: n. sw./n. sp.). A summary diagram depicting the relative abundances of the main taxa (maximum abundance $\geq$5%) is presented in Figure 2. The regional vegetation summary (Figures 2 and 4) is based on the percentage data for all of the 150 species.

It was assumed that the high fern spore count was indicative of a high fluvial contribution to the pollen assemblage, as many of the spores showed obvious signs of long distance transport. Tree ferns are a common component of riparian vegetation in New Zealand forests (Dawson and Lucas 2000) and are likely to be over-represented in river borne pollen derived from a forested catchment. Therefore, in order to provide a more meaningful signal of the regional pollen flux, percentages of the other non-spore palynomorphs were expressed as a fraction of the pollen total minus both the swamp elements (Cyperaceae, etc.) and fern spores.

The Zone analysis in Zone 1.2 (Juggins 1992) resulted in division of the pollen record into 3 main zones (I, II, and III) and 2 sub- zones (Ia and IIIa) (Figures 2 and 4). The zone analysis separated the stratigraphic samples into 20 clusters, but 5 of these clusters possessed a between cluster dispersion that was significantly greater than the remaining 15 clusters. The three clusters with the largest total dispersion (21.8, 18.5, and 16.9) were selected as the main zone boundaries. The 2 sub-zones were based on clusters with total dispersion values of 15.6 and 12.7. The highest total dispersion value for the 15 discarded clusters was 10.4.

Zone I: 120–52 cm. Prumnopitys spp. and Podocarpus zone

Spores from *Cyathea* spp. dominate the n. sw. total, increasing from 60% to 70% at the top of this zone. The n. sw./n. sp. total is dominated by pollen from podocarp/broadleaf canopy trees; *Prumnopitys taxifolia* ($\leq$50%), *Prumnopitys ferruginea* ($\leq$10%), *Podocarpus* spp. ($\leq$10%), and undifferentiated podocarp pollen types ($\leq$50%). *Nothofagus* subgenus *Fuscospora* type is present at an average abundance of 5% of the n. sw./n. sp. total. There is a slight increase in the abundance of Cyperaceae pollen from 5% to 15% of the pollen total at about 100 cm depth.

Zone Ia: 94–52 cm. Leptospermum/Kunzea and Asteraceae zone

This zone is characterised by a decrease in the abundance of *P. taxifolia* from 50% to 5% of the n. sw./n. sp. total. There is also an increase in the abundance of *Leptospermum/Kunzea* spp. and Asteraceae pollen. This is accompanied by a minor increase in the proportion of pollen from *Coriaria* spp., *Astelia* spp., and pollen from various low forest and scrub taxa.

Zone II: 52–31 cm. Poaceae, Pteridium and Apiaceae zone

Cyathea spp. spores decrease in abundance from 70% to 40% of the n. sw. total at the top of this zone. This zone is also characterized by a decrease in the total contribution of podocarp/broadleaf canopy tree pollen from ~85% to ~20% of the n. sw./n. sp. total. This was accompanied by a peak in *Pteridium esculentum* at 33 cm, and an increase in the abundance of pollen from *N. Fuscospora* type; low forest and scrub, including *Pseudopanax* spp.; Apiaceae; Asteraceae and Poaceae, which increases from ~0% to 20% of the n. sw./n. sp. total. There is also a rapid increase in the abundance of charcoal in the pollen samples.

Zone III: 30–0 cm. Poaceae, Pteridium, Pinus and Salix spp. zone

Pollen from two exotic trees; *Pinus* spp. and *Salix* spp., appears at 30 cm and 15 cm respectively. The steady decline of podocarp/broadleaf canopy tree pollen that began at 45 cm continues more gradually, with abundance decreasing from 20% to 10% of the n. sw./n. sp. total at the top of the core. Cyperaceae pollen increases from 15% to ~ 30% of the pollen total at the top of the core.

Zone IIIa: 14–0 cm Salix spp. zone

This zone is characterised by the appearance of pollen from *Salix* spp. There is also a minor increase in Asteraceae pollen, while *Leptospermum/Kunzea* spp. pollen disappears from the record.

Invertebrate paleontology

Abundances of the main invertebrate taxa present in the Lake Forsyth core are presented in Figure 4. The chironomid fauna was dominated by large numbers of head capsules that closely resemble *Chironomus zealandicus* Hudson, a species that was found living in the lake at the time of coring (Figure 3d). The taxonomy of the New Zealand Chironomidae is currently under revision (e.g., Boothroyd 1999 and Boothroyd 2002). Previous classifications of chironomid fauna have been based solely on the characteristics of the male adult, and full associations between all mature and immature life stages are still unknown (Boothroyd 2002). Consequently, there is at least one other species of *Chironomus* in New Zealand that is currently indistinguishable from *C. zealandicus* on the basis of larval headcapsule morphology alone, i.e. *Chironomus analis* Freeman (Shakau 1993). Hence, all the *Chironomus* headcapsules from the core were identified to genus level only, i.e., *Chironomus* spp.

The record was divided into five main zones (1–5), and two sub-zones (2a and 5a) selected from the 20 clusters produced by Zone 1.2 (Juggins 1992) (Figure 4). Zones were selected from the 20 cluster set on the basis of total dispersion values produced in the analysis. Dispersion values ranged from 40.1 (Zone 2/Zone 3 boundary) to 18.5 (Zone 2/Zone 2a boundary) (Figure 4). Of the 13 rejected clusters the highest dispersion value was 12.9.

Zone 1: 120–106 cm. Chironomus spp. and foraminifera zone

This horizon yielded a chironomid head capsule concentration of 2.5 head capsules/g dry sediment, the lowest abundance for the entire core. The chironomid head capsules were derived exclusively from *Chironomus* spp. However there is a relatively diverse assemblage of benthic foraminifera (H' = 0.1 – 0.4). Three species of foraminifera were abundant in this section; *A. p. f. aoteana*, *Elphidium excavatum f. williamsoni* Haynes, and *Zeaflorilus parri* Cushman. *Z. parri* was sparse and only present at the base of the core, while the abundance of *A. p. f. aoteana* and *E. e. f. williamsoni* decreased up-section to the base of Zone 2. The remains of molluscs were abundant in Zone 1, with a

conspicuous concentration in the upper 5 cm of the basal sandy unit. Most common were fragments and one set of attached valves belonging to bivalve *C. stutchburyi*. The gastropods *Potamopyrgus pupoides* Hutton and *Littorina* (*Austrolittorina*) *unifasciata* Philippi were also abundant.

Zone 2: 106–43 cm Chironomus spp. zone

Chironomid head capsules increased in abundance to $\sim$ 10 head capsules/g of dry sediment. The chironomid fauna was still dominated by *Chironomus* spp., with the appearance of low abundances of *Crictocopus* spp. van der Wulp (Figure 3e), *Corynocera* spp. Boothroyd (Figure 3g), and *Tanytarsus vespertinus* Hutton. *A. p. f. aoteana* is present in low concentrations for the bottom $\sim$15 cm of this zone. Upon disappearance of *A. p. f. aoteana* the overall diversity of the biological assemblage drops to 0 at the middle of this zone.

Zone 2a: 56–43 cm: Chironomus spp., Oecetis unicolor zone

The concentration of chironomid headcapsules remains constant while cases and remains from the caddisfly *Oecetis unicolor* (Figure 3a, b and c) are present in small concentrations. Headcapsules from the chironomid genus Tanypodinae (? *Gressittius antarcticus* Hudson) (Figure 3f) are present for the first time in the record. Stellate cell colonies of *Pediastrum simplex* (Figure 3h) appear for the first time in low concentrations at the top of this zone. Overall species diversity increases to 0.25.

Zone 3: 43–33 cm. Chironomus spp., Oecetis, Tanypod and Pediastrum zone

The concentration of chironomid head capsules increases from $\sim$5 to $\sim$20 head capsules/g dry sediment. *Chironomus* spp. still dominated while numbers of Tanypodinae head capsules increased. Larval cases from *O. unicolor* increased at $\sim$ 42 cm yielding 4 cases g^{-1}dry sediment. The abundance of *P. simplex* colonies increases to $\sim$2.5 colonies $\times 10^4$ g^{-1} dry sediment at the top of zone 3. Species diversity peaks at 0.25 at 40 cm then drops to 0.1 at the top of this zone.

Zone 4: 33–15 cm. Chironomus spp. and Pediastrum zone

Chironomid headcapsule abundance remained constant, except for a decline 50 and 55 cm. Tanypodinae head capsules disappeared from the record completely. Four chironomid species remain; *Chironomus* spp., *Tanytarsus funebris* Freeman, *T. vespertinus*, and *Crictocopus* spp. *Oecetis unicolor* cases and remains occurred in low concentrations before disappearing from the record completely at 20 cm. The concentration of *P. simplex* increases to a peak of about 30 colonies $\times 10^{4}$ g^{-1} at 24 cm depth. *P. simplex* concentrations then return to the concentrations that were present in Zone 3. Species diversity remains approximately 0.1.

Zone 5: 15–0 cm: Chironomus spp. zone

Chironomus spp. headcapsules peak initially to the highest concentration for the entire core at 10 cm. This peak is followed by a rapid decline to a low concentration of $\sim$5 headcapsules g^{-1} dry sediment. Overall species diversity drops to 0, with *Chironomus* spp. remaining as the only faunal taxon at the top of the core.

Zone 5a: 8–0 cm. Chironomus spp. low concentration zone

Chironomus sp. headcapsules are present in low concentrations. Species diversity is low.

Numerical analysis

PCA of aquatic species data

Figure 5a and b present PCA plots of axes 1 and 2 of aquatic species and samples respectively, based on 13 aquatic species and 43 stratigraphic samples. A summary of the PCA statistics is presented in Table 1. PCA axis 1 (λ_1 = 0.285) contrasts salt-tolerant benthic foram species to the right of the diagram with high concentrations of *Chironomus* spp. and the freshwater algae *P. simplex* to the left. PCA axis 2 (λ_2 = 0.191) contrasts *O. unicolor*, Tanypodinae and Orthocladinae at the top, with *Crictocopus* spp. and *Tanytarsus* spp. at the bot-

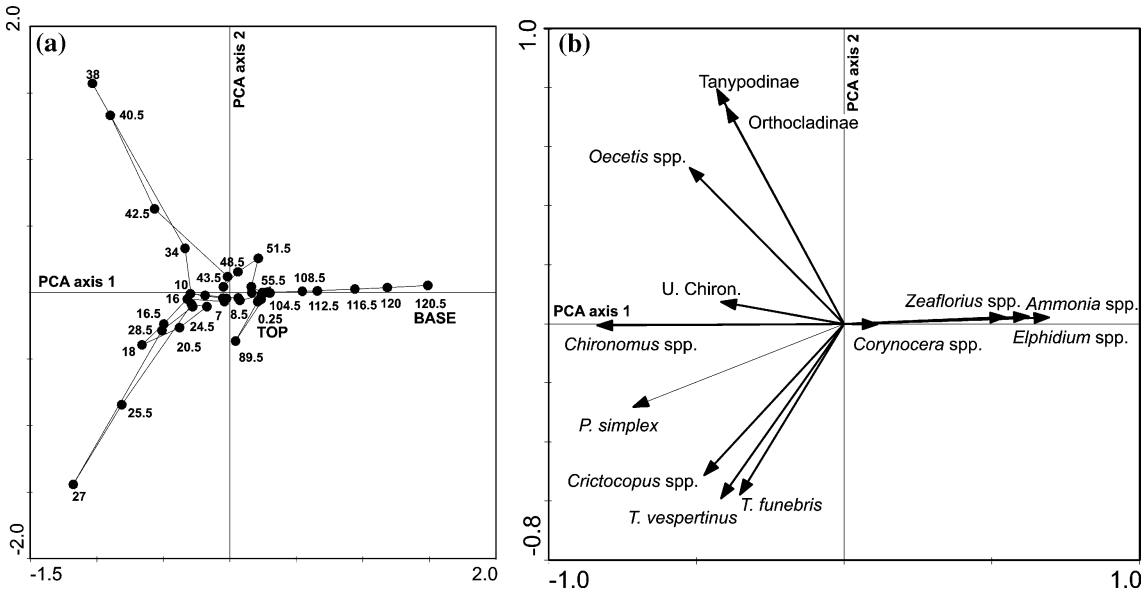

Figure 5. PCA ordination plots of aquatic species and stratigraphic samples. (a) Stratigraphic samples with depths labeled in cm from the top of the core, fitted passively and connected as a series from the base to the top of the core. (b) PCA plot of aquatic species, axis 1 versus axis 2.

Table 1. Summary of the results of the principle components analysis (PCA) of 13 aquatic species from 43 stratigraphic samples.

Axes:	1	2	3	4	Total variance
Eigenvalues	0.285	0.191	0.146	0.111	1.00
Cumulative percentage variance of species data	28.5	47.6	62.2	73.2	
Sum of all eigenvalues					1.00

tom. Large distances between samples on the stratigraphic depth plot Figure 5a) represent major changes in the aquatic fauna. There are two main phases of species composition change. The first major change in species composition occurs between 43.5 and 32.5 cm, which corresponds to faunal Zone 3 in Figure 4. The second main period of species composition change occurs between 28.5 and 24.5 cm which occurs in the middle of faunal Zone 4 in Figure 4.

Redundancy analysis of vegetation/aquatic species relationship

The eigenvalues for the first and second RDA axes were high ($\lambda_1 = 0.223$, $\lambda_2 = 0.167$) and captured 39.0% of the explained variance in the aquatic species data (Figure 6, Table 2). The species–environment correlation for RDA axis 1 was high (0.917) and accounted for 44.1% of the variation in the species–environment relationship. The species–environment correlation for RDA axis 2 was slightly lower than axis 1 (0.808) and accounted for 33.0% of the variation in the species environment relationship. The vegetation class "Podo. sec." (Podocarp/Broadleaf Secondary Trees) was strongly correlated with RDA axis 1; whereas "Herb" (Herbs and Grass), and "Podo. can." (Podocarp Canopy Trees) were strongly correlated to RDA axis 2. "Disturb." (Disturbance Indicators) approximately bisects RDA axis 1 and 2, but shows a slightly higher correlation with RDA axis 2.

The cosine of the angle between species and environmental arrows (here abbreviated to COS) provides a guide to the degree of species environment correlation (ter Braak 1987). High concentrations of *P. simplex* were typical of high percentages of "Disturb" (COS = 0.97) and "Herb" (COS = 0.86). High concentrations of *Chironomus* spp. were strongly associated with high percentages of "Disturb" pollen (COS = 0.98), but showed a higher correlation to

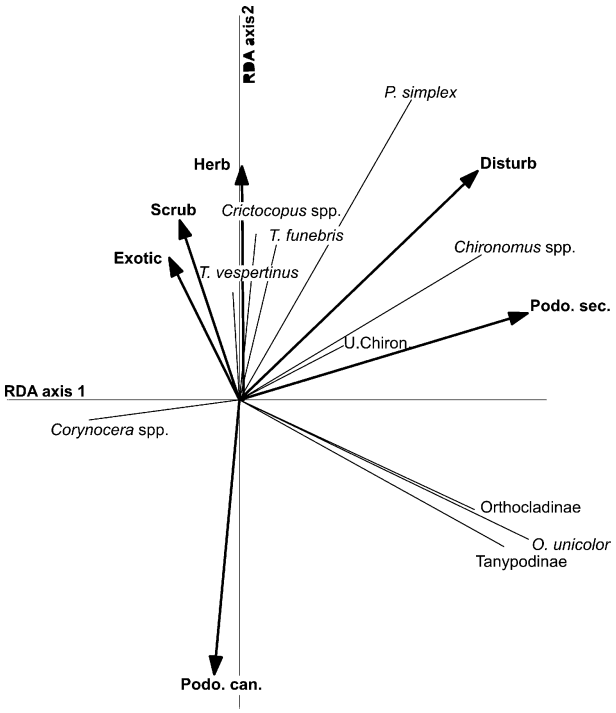

Figure 6. Redundancy analysis (RDA, biplot) of aquatic taxa from the Lake Forsyth fossil record. Analysis includes 22 stratigraphic samples with pollen abundances (%) determined from the pollen record. Disturbance Indicators (Disturb.), Podocarp Secondary Trees (Podo.sec.), Podocarp/Broadleaf Canopy Trees (Podo.can.), Herbs and Grass (Herb), Low Forest and Scrub (Scrub), and Exotic Trees (Exotic). Aquatic species with actual names except for: unidentified chironomids (U. Chiron.).

Table 2. Summary of the results of redundancy analysis (RDA) of aquatic taxa from 22 stratigraphic samples in the Lake Forsyth core constrained to the relative abundances of 6 main pollen types.

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.223	0.167	0.08	0.021
Species–environment correlation	0.917	0.808	0.712	0.502
Cumulative percentage variance				
of species data	22.3	39.0	47.1	49.1
of species–environment relation	44.1	77.1	93.0	97.1
Sum of all canonical eigenvalues				0.560

"Podo. sec" (COS = 0.98) than to "Herb" (COS = 0.46). High concentrations of *Crictocopus* spp. and *Tanytarsus* spp. were inversely related to the percentage of "Podo. can." pollen (COS ~ -1), but showed a high positive correlation with the percentage of "Herb", "Scrub", and "Exotic" pollen (COS ~ 1, 0.9, and 0.78 respectively). Concentrations of Orthocladinae, *O. unicolor*, and Tanypodinae approach an inverse relationship to the percentage of "Exotic", "Scrub", and "Herb" pollen (COS ~ -0.6). These species show a positive correlation to both "Podo. can." and "Podo. sec." with a slightly stronger correlation to the percentage of "Podo. sec." (COS ~ 0.34 and 0.7 respectively).

When the species data were constrained to only one environmental variable (pollen class) (Table 3), the largest statistically significant explanatory

Table 3. Summary of partial RDA of the faunal aquatic species assemblages from the Lake Forsyth core.

Variable	RDA		
	λ 1/λ 2	Variance (%)	*P*
Disturb.	0.575	15.2	0.001
Podo.sec.	0.516	14.2	0.001
Podo.can.	0.364	10.1	0.002
Herb	0.320	9.1	0.001
Scrub	0.321	9.0	0.009
Exotic	0.161	4.7	0.172

The ratio of the first constrained eigenvalue (λ_1) to the second unconstrained eigenvalue (λ_2), and percentage variance explained by relative abundances for each pollen class. Disturbance Indicators (Disturb.), Podocarp Secondary Trees (Podo. Sec.), Podocarp/Broadleaf Canopy Trees (Podo. can.), Herbs and Grass (Herb), Low Forest and Scrub (Scrub), and Exotic Trees (Exotic).

power was captured by "Disturb" (15.2%), followed by "Podo. sec." (14.2%), and "Podo. can." (10.1%).

Interpretation and discussion

The early history of the Lake Forsyth Basin: a tidal estuary

Both the sedimentology and paleoecology imply that the Lake Forsyth Basin was once a tidal estuary, with a direct opening to the Pacific Ocean. This is not surprising, considering the proximity of the lake to the present coastline, and the historical accounts from the mid 19th century which mention a channel connecting Lake Forsyth to the Pacific Ocean (Soons 1998). *Chione (Austrovenus) stutchburyi* lives intertidally and in subtidal estuarine and harbour settings (Beu et al. 1990), while *Potamopyrgus pupoides* inhabits the brackish lower reaches of streams, rivers and tidal estuaries (Powell 1979). *P. pupoides* is extant in the Avon Heathcote Estuary to the north of Banks Peninsula (Figure 1). *Zeaflorilus parri* is a typical component of shallow, wave dominated nearshore foraminiferal assemblages around many parts of New Zealand (Hayward et al. 1996); while an *Ammonia-Elphidium* association occurs widely around New Zealand in sheltered, intertidal mud and sand flats, and beaches (Hayward and Hollis 1994). The overall assemblage in faunal Zone 1 probably represents mixing of death assemblages from the inner reaches of a Forsyth embayment with material from near the mouth of the bay.

The transition from a *Zeaflorilus-Ammonia-Elphidium* foraminiferal fauna in faunal Zone 1 to an exclusively *A. p. f. aoteana* fauna at the base of faunal Zone 2 (Figure 4) indicates a partial closing off of the Forsyth Basin and a transition to a less saline and lower energy environment. The lower energy interpretation is supported by the disappearance of large shell fragments that are present at the base of the core and the gradual reduction and then elimination of sand from the sediments. The overall reduction in salinity is suggested by the reduction in foram diversity at the base of faunal Zone 2. The remaining foram species, *A. p. f. aoteana*, is widely distributed in brackish and very slightly brackish environments (Hayward and Hollis 1994). This species is not restricted to brackish environments and may occur in virtually fresh water settings near river and stream mouths that periodically flood (Jorissen 1988).

The reduction of salinity is also supported by both the increase in the abundance of *Chironomus* spp. head capsules and the increase in the proportion of Cyperaceae pollen in the record (Figures 2 and 4). The upper salinity limit for *Chironomus zealandicus* larval survival is no greater than 17.5‰ (Robb 1966), demonstrating than at least part of the basin was not fully marine. The salinity records are compatible with either segmentation of environments within the basin or partial blocking (either in space or time) of the embayment by a barrier. The sediment record which comes from close to the mouth strongly suggests the latter.

Basal chronology and the closure of the Lake Forsyth Basin

After the disappearance of *A. p. f. aoteana* at 90 cm there is no evidence of an open marine

connection. From this point on the Forsyth Basin contains a lake that was at least partially protected from a marine influence by the formation of a barrier. Barrier blocked lakes are a common phenomenon on the southern flank of Banks Peninsula (e.g., Soons et al. 1997; Shulmeister et al. 1999) and are created by littoral drifting of sediment from the south under the influence of the persistent Southland Current.

Determining the timing of formation of the barrier is more problematic. Work by Armon (1974) and Shulmeister et al. (1999) have demonstrated that the Kaitorete 'Spit' was substantially in place by about 8000 years BP and was emplaced during the early Holocene transgression. Soons et al. (1997) dated the most recent closure of the Kaitorete Barrier to ~450 years BP. This date is based on a radiocarbon age from shell hash at a marine/non-marine transition in a core from Birdlings Valley, approximately 4 km west of the Lake Forsyth Core (Figure 1). Soons et al. (1997) believe that the Kaitoreti Barrier has opened and closed several times in the past in response to the avulsions of the Waimakariri River, north and south of Banks Peninsula. Barrier closure is only possible when the Waimakariri River flows north of the peninsula, as it does today. This is important for the Forsyth Basin because gravels can only reach the Forsyth valley mouth if the Kaitorete Barrier is closed.

An AMS radiocarbon date on a bulk sediment sample from about 1.1 m down core, yielded a calibrated radiocarbon date of 7314–7252 year BP (NZA 18809). Consequently, the sandy sediments at the base of the core were probably emplaced during the final phases of the Holocene transgression (Gibb 1986), when the Forsyth Basin was flooded by rising sea-levels. The radiocarbon date was taken from 4 cm below the transition from marine to estuarine conditions, and about 17 cm below the final disappearance of *A. p. f. aoteana* at 90 cm. It seems likely that the final closure of the Lake Forsyth Basin occurred slightly after the isolation of Birdlings Valley from the ocean (which occurred ~450 year BP) as the Kaitoreti barrier would have migrated from west to east (Soons et al. 1997).

Consequently the period between the Holocene transgression and the partial closure of the basin is poorly represented in the sediment record. This could be the result of a long-term very low sedimentation rate in the bay, but is more likely to indicate that tidal sweeping of the bay prevented significant sediment accumulation. Fenster and Fitzgerald (1996) found evidence for reworking of older material following the Holocene marine transgression in a sedimentary sequence from the lower Kennebec River estuary in Maine. Modern studies in similar settings have shown that frequent periods of low deposition and erosion are common (Fan et al. 2002) and often the net sediment transport may be towards the estuary mouth (Fenster and Fitzgerald 1996).

Other cores taken from this area provide further evidence for major periods of erosion following the last marine transgression. Soons et al. (1997) have investigated sediments in valleys on the southern side of Banks Peninsula (Figure 1). In these valleys a fill associated with an early Holocene transgression (dated to between 8000 and 7000 year BP) is unconformably overlain by very late Holocene (< 1000 year BP) barrier, estuarine and lacustrine sediments. Harvey (1996) attributed unexpected old radiocarbon dates in cores taken from the shores of Lake Ellesmere (Figure 1) to contamination by old carbon. However, the chronologies from the Lake Ellesmere cores closely match those of Soons et al. (1997) and the core from Lake Forsyth, suggesting that these "old" radiocarbon ages are in fact real ages.

Despite the complexity of the chronology, there is little doubt that the narrow channel separating Lake Forsyth from the ocean was in place well before the arrival of Europeans c. 1840, which is signalled by the podocarp/broadleaf pollen decline at 48 cm in the core. It is also possible that the major change in stratigraphy to increased herb detritus at 63 cm could be a signal for human arrival and there is some lag in the response of the pollen record to deforestation (this is explained in the following section).

The appearance of Tanypodinae in faunal Zone 2a possibly indicates the stabilization of Lake Forsyth as a freshwater system. There is a limited amount of data available on the salinity tolerance of New Zealand species of Tanypodinae. However, Stout (1985) noted the absence of Tanypodinae from Lake Leg of Mutton, a highly saline coastal South Island lake near Kaikoura. Stout (1985) found that in this situation, *Chironomus*

spp. was the dominant taxon as is the case in the Lake Forsyth core.

Human impact on the Lake Forsyth catchment and adjacent areas

Pre-human vegetation

The pre-Maori settlement vegetation on Banks Peninsula consisted of a continuous cover of podocarp-broadleaf forest, comprising the emergent podocarps kahikatea (*Dacrycarpus dacrydioides* Laubenfels, Quinn and Keng), lowland totara (*Podocarpus totara* Allan), and matai (*Prumnopitys taxifolia* Laubenfels, Quinn and Keng) over a broadleaf canopy. At higher altitudes the vegetation was dominated by thin barked totara (*Podocarpus hallii* Allan) with stands of southern beech forest (mainly *Nothofagus fusca* Hook) on the southeast side of the Peninsula (Wilson 1993). This reconstruction is consistent with Holocene pollen records from Gebbies Valley on the south-west flank of the Peninsula (Soons et al. 2002) and with the findings of this study.

The consistently high values of fern spores in the Lake Forsyth record are interpreted to reflect a significant contribution of river transported pollen into the Lake Forsyth Basin. Bonny (1978) found that up to 85% of the pollen found in lakes with inflowing streams has been transported by flowing water. Dunbar et al. (1997) specifically identified tree fern spores as preferentially transported via the river systems into Wellington Harbour. Many of the fern spores in the Lake Forsyth core showed signs of transport and were typically abraded in appearance, reflecting long-distance transportation. We conclude that this is a result of the dominance of fluvially transported palynomorphs in this record. Dunbar et al. (1997) also noted that changes in vegetation in response to anthropogenic influences had been "diluted" by the mass of palynomorphs recycled from soils and those sourced from distal parts of their catchment that escaped clearance. Consequently there was a delayed response to deforestation by pollen records from cores taken from settings with a high fluvial contribution.

Human disturbance in the catchment

Maori disturbance. New Zealand has a relatively short history of human occupation. The Maori people arrived in New Zealand from Eastern Polynesia between 1200 and 1400 AD (McGlone and Wilmshurst 1999). Pollen analysis from numerous sites around New Zealand (e.g., McGlone et al. 1995; Elliot et al. 1997; Horrocks et al. 2002) indicate that this first wave of human colonizers dramatically reduced the area of native forest cover. The Maori people used fire during moa hunting (Scott 1999), as a means of land clearance, and to encourage the growth of bracken (*Pteridium esculentum* Forster) (McGlone 1989). Consequently a Maori disturbance signal in the pollen record can be inferred by a decline in canopy tree pollen, a major increase in the quantity of *P. esculentum* spores, an influx of charcoal particles, followed by the appearance of pollen from colonizing species such as *Coriaria* spp. (McGlone and Wilmshurst 1999).

Radiocarbon dating of moa-hunting sites suggests the presence of Maori settlers on Banks Peninsula by 1300 AD (Challis 1995). It has been predicted that as much as a third of the pre-Maori forest cover was destroyed prior to the arrival of Europeans in the area in 1840 (Soons et al. 2002). Pollen analysis of a core from Travis Swamp, Christchurch (Figure 1) (McGlone 1995, cited in McGlone and Wilmshurst 1999) shows evidence for major Maori deforestation beginning between 1218 and 1397 AD.

There is no definitive evidence in the Lake Forsyth pollen record for significant pre-European deforestation. There are several very minor peaks of *Pteridium esculentum* between 120 and 90 cm core depth, and there is an isolated increase in Asteraceae and *Leptospermum*/*Kunzea* spp. which is accompanied by a minor decline in the abundance of canopy tree pollen at about 80 cm depth. In the absence of major changes disturbance indicating taxa, the relative lack of charcoal, and the propensity of eastern South Island, New Zealand to be subject to natural disturbance due to drought, the presence of a Maori disturbance signal is inconclusive.

European forest clearance and pastoral farming. The widespread deforestation of Banks Peninsula, and the subsequent conversion of large tracts of land to pastoral farming after 1860 is well documented (Petrie 1963). The period of deforestation is represented in the pollen record by the major decline in canopy tree pollen, accompanied by a peak in charcoal and *P. esculentum* at the end of

pollen Zone II. The establishment of grassland and the planting of exotic trees is evident in pollen Zone III, and is expressed as a major increase in Poaceae pollen. Foweraker (1927) mentions the planting of large stands of mixed conifers (including *Pinus* spp.) in the Canterbury region around 1870. Dunbar et al. (1997) found there was a delay of 25 years between the first planting of *Pinus radiata* D. Don in 1865 in Wellington, New Zealand, and its appearance in the pollen record about 1890. The first appearance of *Pinus* spp. pollen in the Lake Forsyth record post dates deforestation, which was largely completed by 1880 (Petrie 1963). It seems reasonable to assume a similar delay in the appearance of *Pinus* spp. in the Lake Forsyth pollen record, and a date of 1895 is assigned to the first appearance of *Pinus* spp. in the record (Figures 2 and 4).

The influence of land-use changes on the aquatic ecosystem. Results from redundancy analysis (RDA) (Figure 6, Tables 2 and 3) reveal a strong correlation between changes in regional vegetation and the concentrations of the main aquatic taxa. It appears that deforestation resulted in conditions in the lake that encouraged the appearance, and increase in abundance of the aquatic invertebrate taxa, particularly *Chironomus* spp. beginning in faunal Zone 2a and peaking in faunal Zone 3. Results from the principle components analysis (PCA) (Figure 5a and b) show a period of dramatic change in the aquatic species assemblage between ~ 43 and 20 cm. This corresponds with a pulse of increased diversity between $\sim$50 and 35 cm, and the period of deforestation recorded in the pollen record in pollen Zone II (Figures 2 and 4).

This change in the aquatic taxa probably reflects an initial low input of nutrients into the lake coupled with a reduction in salinity. This is supported by the appearance of low concentrations of colonies from *P. simplex* at the faunal Zone 2/Zone 3 transition. Yasuda et al. (2000) discovered a similar increase in *Pediastrum* following deforestation in a core from the Ghab Valley in Northwest Syria. Patterson et al. (2002) also found a strong correlation between *Pediastrum* abundance and the levels of other high nutrient proxies in a core from Swan Lake, Ontario. Critically, *Pediastrum* only blooms in freshwater and this confirms that erosion of the catchment and increased run-off created virtually freshwater conditions in the basin. Historical records state that there was at least a temporary connection between Lake Forsyth and the ocean up until 1843 (Soons 1998). It is quite likely that the isolation of the lake from the ocean also contributed significantly to the reduction in salinity.

Salinity was probably the main determinant of aquatic biological diversity prior to the isolation of the lake from the ocean, and the initiation of deforestation. These changes temporarily changed the aquatic system to one that was primarily driven by the availability of nutrients and dissolved oxygen. This initial reduction in salinity favoured the survival of the Tanypodinae and larvae from the caddis fly *Oecetis unicolor*. Both of these taxa are a common component of many of New Zealand's freshwater oligo-mesotrophic lakes (Stark 1981; Timms 1982 and 1983; Schakau 1991).

The massive increase in the abundance of *P. simplex* and the disappearance of Tanypodinae and *O. unicolor* in faunal Zone 4 suggests a continuation of the low salinity phase, with a switch to a highly productive system. Both the Tanypodinae and *O. unicolor* are absent from shallow highly productive lakes (Stark 1981; Timms 1982 and 1983; Schakau 1991). Patterson et al. (2002) proposed that a similar *Pediastrum* peak in a core from Swan Lake Ontario reflected the increased use of chemical based fertilizers after World War 2. The *Pediastrum* 'bloom' postdates 1895 AD, a date inferred by the appearance of *Pinus* spp. in the record. An estimate based on constant sediment accumulation and slight compaction places the *Pediastrum* peak at 1910 to 1930. Intensive use of aerial topdressing did not occur in New Zealand until 1950 (Alexander and Tullett 1967). Main (2002) also mentions that the first *Nodularia spumigena* bloom was reported in Lake Forsyth in 1907, well before the intensive use of fertilizers after World War II. It seems likely that the increased nutrient input resulting from increased erosion following deforestation, coupled with the increase in dairy farming in the area in the early part of the 20th century (Main 2003) was enough to stimulate a major *Pediastrum* peak, and initiate blooms of *N. spumigena*.

The introduction and proliferation of the black swan (*Cygnus atratus* Latham) in New Zealand in the early 19th century (Mitchell and Wass 1996) may also have contributed to high nutrient levels and algal blooms in the lake. Waterfowl faeces contain a low ratio of N to P (Mitchell and Wass 1995) which may also favour the proliferation of

cyanobacteria in lakes where the faecal component of the nutrient load is large.

Increased catchment erosion also increased the sedimentation rate in the lake from a pre 1840s rate of 0.88 to 3.7 mm/year, a 4-fold increase. It does not appear that an increased sedimentation rate by itself had a negative affect on the survival of aquatic invertebrate taxa. It is quite possible that an input of fine material favoured *Chironomus* spp., which has a preference for a fine muddy substrate (Boubee 1983). Warwick (1980) also proposed that increased levels of sediment input may benefit predatory chironomids (Tanypodinae) when other invertebrates are forced out of the sediments and become vulnerable to predation.

The major decline in the abundance of both *P. simplex* and *Chironomus* spp. is probably indicative of a recent increase in salinity. Lake Forsyth is artificially opened to prevent flooding of the Christchurch-Akaroa highway after periods of high rainfall (Soons 1998). During the period of 1999–2003 salinity reached extreme values of up to 11‰ during the spring and autumn, following the opening of the lake (Canterbury Regional Council, unpublished data). Robb (1966) found that salinities of this magnitude increased the mortality of *Chironomus* spp. larvae. It is likely that such high salinities are responsible for the low chironomid diversity and may have a detrimental effect on other aquatic flora and fauna. Increased salinities may also favour the massive blooms of *N. spumigena*. *N. spumigena* not only benefits from increased nutrient levels, but is also halotolerant (Mazur 2003). Increased nutrient input coupled with increased salinity may have allowed *N. spumigena* to outcompete other species of planktonic algae, including *P. simplex*, resulting in algal blooms. Extensive cyanobacteria blooms seriously affect water quality in that they cause deoxygenation and produce hydrogen sulphide (Mazur 2003). Consequently, frequent *N. spumigena* blooms may have accelerated the decline in water quality.

Conclusion: directions for future management

This paleolimnological study shows the natural development of the Lake Forsyth basin from a tidal coastal embayment ~7000 years BP to a barrier blocked lake, partially isolated from the ocean about 500 years BP. The lake was permanently isolated from the ocean after the arrival of Europeans in the area c. 1840. It appears that human activities over the last 150 years have resulted in three main effects that could be distinguished from signals of natural coastal evolution; salinity changes, increased sedimentation rate, and increased nutrient inputs. A program for the future restoration of this lake should target these areas. The following section examines these points in more detail.

Deforestation led to an increased overland flow and an increased input of freshwater into the lake. As the start of deforestation coincided with the natural isolation of the lake from the ocean it is difficult to determine how much of this salinity reduction was natural and hence set a baseline level for salinity in this lake. It is certain, however, that the recent practice of artificially breaching the gravel barrier separating the lake from the ocean has led to large salinity fluctuations that have a detrimental effect on most of the aquatic fauna. It is necessary to maintain lake levels to prevent flooding of nearby roads and farmland. An alternative method of lake level control that prevents backwash of saline water into the main basin and allows the return migration of eels from the ocean should be investigated.

It is also quite clear that land clearance and ensuing pastoral farming practices have led to an increase in the inflow of nutrients and suspended sediments, resulting in a 4-fold increase in sedimentation rates and blooms of the toxic cyanobacteria *Nodularia spumigena*. A primary directive for future restoration of this system should be watershed nutrient and sediment reduction strategies. The restoration of the wetland at the head of the lake may serve as a natural filter to aid the removal of nutrients and suspended solids transported from the catchment via the Okana and Okuti rivers. Replanting of the steep slopes to the north and south of the lake may also serve to reduce sediment input. The lake may take some time to respond to these measures; since Lake Forsyth is shallow (<4 m maximum depth) it is likely that nutrients stored in the surface sediments will be resuspended by wind disturbance.

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ORIGINAL PAPER

New Zealand chironomids as proxies for human-induced and natural environmental change: Transfer functions for temperature and lake production (chlorophyll *a*)

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Abstract The analysis of chironomid taxa and environmental datasets from 46 New Zealand lakes identified temperature (February mean air temperature) and lake production (chlorophyll *a* (Chl *a*)) as the main drivers of chironomid distribution. Temperature was the strongest driver of chironomid distribution and consequently produced the most robust inference models. We present two possible temperature transfer functions from this dataset. The most robust model (weighted averaging-partial least squares (WA-PLS), $n = 36$) was based on a dataset with the most productive (Chl $a > 10$ μg l^{-1}) lakes removed. This model produced a coefficient of determination (r^2_{jack}) of 0.77, and a root mean squared error of prediction ($RMSEP_{jack}$) of 1.31°C. The Chl *a* transfer function (partial least squares (PLS), $n = 37$) was far less reliable, with an r^2_{jack} of 0.49 and an $RMSEP_{jack}$ of 0.46 $Log_{10}\mu g\ l^{-1}$. Both of these transfer functions could be improved by a revision of the taxonomy for the New Zealand chironomid taxa, particularly the genus *Chironomus*. The *Chironomus* morphotype was common in high altitude, cool, oligotrophic lakes and lowland, warm, eutrophic lakes. This could reflect the widespread distribution of one eurythermic species, or the collective distribution of a number of different *Chironomus* species with more limited tolerances. The Chl *a* transfer function could also be improved by inputting mean Chl *a* values into the inference model rather than the spot measurements that were available for this study.

Keywords Chironomids · New Zealand · Transfer function · Temperature · Chlorophyll *a*

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Introduction

The Dipteran family Chironomidae (non-biting midges) is the most widely distributed and frequently the most abundant group of insects in freshwater (Armitage et al. 1995). Taxon abundance, coupled with short life cycle duration, make this group an ideal target for use in paleolimnological studies (Walker 1995, 2001). As such, chironomids have been used extensively in the Northern Hemisphere in paleoenvironmental research to reconstruct climate change and to quantify the effects of human impact on lake ecosystems (e.g. Brooks and Birks 2000, 2001; Brooks et al. 2001; Quinlan and Smol 2002).

Paleoenvironmental analysis using chironomids is sparse in New Zealand, consisting of early qualitative work (Deevy 1955) and some later

more quantitative efforts (Boubee 1983; Schakau 1986, 1991, 1993) that attempted to determine the ecological tolerances of the New Zealand chironomid taxa. None of the earlier New Zealand investigations resulted in the production of quantitative inference models. Information derived from lake classification and ordination was applied to down-core chironomid fossil data, but the modern ecological results were applied qualitatively. Furthermore, the studies by both Boubee and Schakau were limited either by altitude and/or the length of the nutrient gradient covered by the 'training set'. Neither of the studies collected chironomid remains from lakes situated above the tree-line (~1000–1300 m a.s.l.).

Since those studies were completed, there has been major progress in the use of statistics in paleoecological research, and a major improvement in the resolution of the taxonomy of the New Zealand chironomid taxa, particularly the Orthocladiinae (see Boothroyd 1994, 1999, 2002). Despite these developments, there has been no attempt to develop chironomid-based inference models to enable the quantitative reconstruction of past environmental conditions. The most recent application of chironomids for paleoenvironmental reconstruction in New Zealand (Woodward and Shulmeister 2005) was still limited to making qualitative generalisations on past environmental conditions based mostly on the work of Boubee (1983) and Shakau (1986, 1991, 1993).

This paper presents preliminary transfers functions for temperature and lake production (chlorophyll *a* (Chl *a*)) based on chironomid data from a training set of 46 New Zealand lakes (Fig. 1). These are the first chironomid-based transfer functions to be developed in the Southern Hemisphere, although work is also underway to develop a temperature transfer function based on a larger training set with a deliberately reduced trophic gradient (M.J. Vandergoes et al. unpublished).

The impetus for this work comes from two sources:

Firstly, New Zealand paleoclimate history has become a focus for international studies, because New Zealand is seen as a good distal location to test paleoclimate hypotheses developed from Northern Hemisphere data (e.g. Broecker 1997). This is particularly true for the time interval from the last glacial maximum (ca. 21,000 years ago) to the start of the present interglacial (ca. 11000 years ago). Many studies of glacial systems (e.g. Denton and Hendy 1994; Shulmeister et al. 2005) and biotic indicators, notably pollen (e.g. McGlone et al. 2004; Vandergoes and Fitzsimons 2003) have been undertaken to investigate these changes but are limited by inadequate or contradicting estimates of temperature change.

Recently, there has been a focus on developing new quantitative paleoclimate tools for use in New Zealand. Transfer functions have been developed for phytoliths (Prebble et al. 2002) and testate amoebae (Wilmshurst et al. 2003) while bioclimatic modelling approaches have been applied to beetles (e.g. Marra et al. 2004). For some of these proxies (e.g. phytoliths) the inference of climate parameters from the data is not straightforward, while with others (e.g. testate amoeba) reconstructions appear to be affected by preservation biases. New, high resolution and widely applicable proxies are needed to test patterns of inferred climate change. Studies in the Northern Hemisphere have shown that even though chironomids are aquatic invertebrates, they can be used to reliably infer past air temperatures, and hence track climate change (e.g. Lotter et al. 1997; Brooks and Birks 2000). Hence, the development of a proxy for air temperature for a southern latitude land mass (New Zealand) will lead to the acquisition of critical data concerning climate change in this region during the Late Quaternary.

Secondly, there is growing concern in New Zealand about damage to waterways from changed agricultural practices (notably dairying in dry-land areas) and urbanisation. Even though a relatively small percentage of the lakes in New Zealand can be classified as eutrophic (22%) or hypertrophic (18%) (Taylor and Smith 1997), local councils have initiated 'long-term' water quality monitoring programmes (e.g. Burns and Rutherford 1998) and developed strategies and targets to facilitate the restoration of 'damaged' ecosystems (e.g. Hamilton 2003; Rutherford 2003). However, rigorous scientific

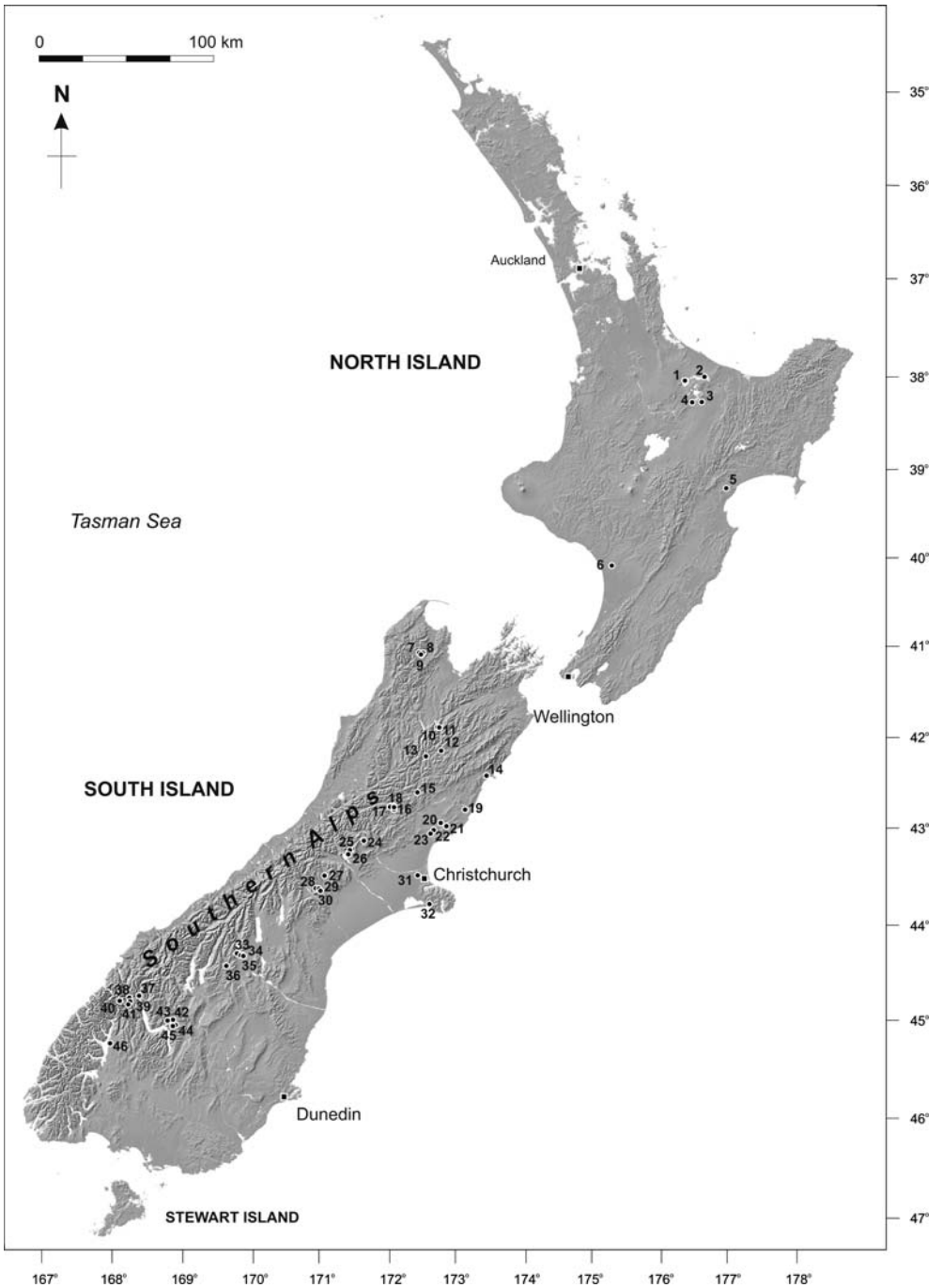

Fig. 1 Map showing the distribution of the 46 study lakes in New Zealand. Numbers refer to lakes listed in Table 1

monitoring of lakes and estuaries in New Zealand only extends back as far the early 1980s (Taylor and Smith 1997) and there are few continuous records of physical and chemical parameters. Therefore, it is difficult to establish base-line levels for lake productivity and set reasonable targets for lake restoration in the absence of long-term records.

Many studies in the Northern Hemisphere have successfully used transfer functions based on

biological proxies (e.g. chironomids and diatoms) to extend lake records beyond historical time. These long-term paleolimnological records (in tandem with other proxies, e.g. palynomorphs) provide valuable information on the natural functioning of lake/catchment systems and their response to anthropogenic disturbance (deforestation and intensive farming) (e.g. Bennion and Appleby 1999; Brooks et al. 2001; Kauppila et al. 2002; Quinlan and Smol 2002; Langdon et al. 2006). At this stage there is only one other robust published transfer function that is capable of quantifying past lake production (Chl *a*) in New Zealand (Reid 2005). Reid (2005) also produced diatom-based transfer functions for total phosphorus (TP) and dissolved reactive phosphorus (DRP), but these did not perform as well as the Chl *a* transfer function. The addition of a second, chironomid-based transfer function for lake productivity will allow comparison and cross validation between the chironomid and diatom-based transfer functions.

Description of sites studied

The training set comprised 46 lakes located in the North and South Island of New Zealand (38.04°S to 45.12°S latitude, 167.49°E to 176.16°E longitude) (Fig. 1, Table 1) The climate in this region is generally mild and oceanic. However, there are large temperature and precipitation gradients in the New Zealand region, particularly in the South Island. This is a product of the rugged topography of the Southern Alps and the influence of this mountainous terrain on the predominantly westerly airflow over the southern part of the country (Sturman and Wanner 2001). Orographic uplift of the airflow off the Tasman Sea results in an extreme contrast in average rainfall between the western and eastern sides of the mountains. Average annual precipitation near the divide on the western side of the Southern Alps can reach over 10,000 mm, while the eastern coastal plains and mountain basins receive an average annual rainfall of 600 mm (Griffiths and McSaveney 1983). Elevation of the sample sites ranges from 20 to 1880 m a.m.s.l. (above mean sea level), corresponding to estimated late summer (February) mean air temperatures of 8.2–18.1°C (Table 1).

The catchment vegetation of all the sample locations in the North Island and those located on the eastern coastal plains and foothills (below ~450 m a.m.s.l.) of the South Island has been subjected to intensive human modification. The original podocarp/broadleaf forest (e.g. *Podocarpus*, *Prumnopitys*, and *Dacrydium cupressinum*) cover in these areas has been largely cleared, firstly by Polynesian settlers, and more recently by Europeans to make way for pastoral farming (Ogden et al. 1998). Catchment vegetation of the lakes in these areas now comprises low scrub (e.g. *Discaria toumatou*, *Coprosma*, and *Leptospermum*), exotic trees (e.g. *Pinus radiata*), and introduced pasture grasses (e.g. *Pennisetum clandestinum*).

At higher altitudes up to the tree-line (~1000 to 1300 m a.m.s.l.) the natural vegetation comprises beech forest (four endemic species of *Nothofagus*) except for in the mid-central South Island 'Beech Gap' where podocarp/hardwood forests (e.g. *Podocarpus*) give way to other conifers (*Libocedrus*, *Phyllocladus*, and *Halocarpus*) at higher altitudes up to the tree-line. This natural forest cover now only exists in conservation reserves, and in remote, rugged un-farmed areas. Cleared forest has been replaced by indigenous grassland (montane tussock-land; e.g. *Poa*). Large tracts of this land are now used for low density sheep farming. Above the tree-line, forest and scrub gives way to sub-alpine tussock (e.g. *Chionochloa*) and other alpine flora (e.g. Asteraceae, Gentianaceae, and Ranunculaceae). Introduced grasses and composite weeds have also invaded this zone but less successfully than at lower elevations.

Methods

Forty-six lakes, selected to maximize the gradients of trophic status and temperature, were sampled in New Zealand during the summers (December to February) of 2002/2003, 2003/2004, and 2004/2005 (Fig. 1 and Table 1). Surface sediment samples, physical measurements and

Table 1 Lake number (nr) (corresponding to map, Fig. 1) and respective lake name

Lake Nr	Location	Lat (°S)	Long (°E)	Altitude (m)	Feb mean (°C)	Lake area (km^2)	Depth (m)	Secchi depth (m)	Cond ($\mu S\ cm^{-1}$)	NO_x-N (mg/l)	React P (mg/l)	TN (mg/l)	TP (mg/l)	Chl *a* ($\mu g/l$)	TC (mg/l)	DIC (mg/l)	DOC (mg/l)	Ca (mg/l)	Mg (mg/l)	Na (mg/l)	K (mg/l)	Cl (mg/l)	SO_4 (mg/l)	HC count	# Taxa
1	Lake Rotorua N	38.04	176.16	280	17.8	79.780	20.50	2.030	200.00	0.0005	0.0220	0.5905	0.0660	32.10	–	–	–	–	–	–	–	–	–	67	8
2	Lake Rotoehu	38.01	176.31	295	17.6	8.110	10.00	2.040	150.00	0.0180	0.0230	0.7100	0.0600	25.00	–	–	–	–	–	–	–	–	–	114.5	8
3	Lake Rerewhakaaitu	38.17	176.29	435	16.8	7.470	14.00	4.500	30.00	0.0040	0.0010	0.3400	0.0100	3.60	–	–	–	–	–	–	–	–	–	216.5	14
4	Lake Okaro	38.17	176.23	412	17	0.280	16.00	2.440	91.90	0.0110	0.0164	0.8765	0.0283	5.79	–	–	–	–	–	–	–	–	–	63	7
5	Lake Tutira	39.13	176.53	150	18.1	1.470	40.00	5.600	127.88	0.0430	0.0010	0.1047	0.0069	3.82	–	–	–	–	–	–	–	–	–	119.5	10
6	Lake Dudding	40.06	175.16	86	17.5	0.130	12.00	2.600	125.30	0.0280	0.0226	1.3185	0.0589	19.11	–	–	–	–	–	–	–	–	–	68	8
7	Iron Lake	41.06	172.36	1463	10.2	0.068	21.00	8.100	17.70	0.0220	0.0050	0.0700	0.0100	0.50	3.700	1.500	2.100	2.200	0.360	1.240	0.100	1.780	0.200	89	6
8	Lake Sylvester	41.06	172.37	1333	10.9	0.266	24.20	6.900	26.70	0.0190	0.0030	0.0500	0.0300	0.40	4.400	2.500	1.800	3.300	0.710	1.310	0.070	1.460	0.200	56.5	9
9	Little Sylvester Lake	41.06	172.37	1333	10.7	0.076	14.00	4.000	42.40	0.0210	0.0030	0.0900	0.0300	0.40	7.300	4.300	3.000	5.900	1.160	1.340	0.030	1.430	0.200	59.5	14
10	Rainbow Skifield W	41.52	172.51	1690	9.8	0.052	10.10	9.500	10.10	0.0190	0.0030	0.0800	0.0100	0.70	2.900	1.100	1.800	1.200	0.150	0.830	0.170	0.360	0.200	337	8
11	Rainbow Skifield E	41.53	172.52	1479	10.5	0.028	4.50	4.500	26.30	0.0180	0.0030	0.0600	0.0300	0.20	4.300	2.700	1.600	4.800	0.150	1.050	0.110	0.190	1.400	111.5	7
12	Lake Sedgemere	42.08	172.54	1008	12.9	0.080	1.30	1.300	30.90	0.0040	0.0375	0.3996	0.0427	0.50	10.597	4.103	6.494	3.447	1.015	2.814	0.600	0.986	0.378	235.5	16
13	Princess Bath	42.11	172.41	1757	9	0.070	15.50	10.500	13.40	0.0180	0.0030	0.1200	0.0100	2.30	2.600	1.400	1.100	2.200	0.090	0.630	0.020	0.020	0.500	81	3
14	Lake Rotorua S	42.24	173.34	20	17.3	0.550	2.08	0.380	185.00	0.0188	0.0269	6.0750	0.4529	15.30	56.987	2.850	54.137	5.887	3.178	20.891	1.965	23.702	0.200	104	13
15	Horseshoe Lake	42.35	172.31	468	15.4	0.040	10.30	3.700	83.70	0.0131	0.0087	0.4726	0.0100	0.40	16.076	8.132	7.944	10.693	2.181	6.693	1.065	3.098	3.160	331.5	13
16	Lake Taylor	42.46	172.13	588	14.1	1.850	35.00	6.650	53.00	0.0011	0.0030	0.1434	0.0069	2.27	–	–	–	–	–	–	–	–	–	134.5	11
17	Lake Mason	42.44	172.10	329	14.1	1.000	37.00	6.400	61.90	0.0009	0.0009	0.1054	0.0100	1.11	–	–	–	–	–	–	–	–	–	53.5	14
18	Lake Sheppard	42.45	172.15	587	14.6	1.150	17.00	1.450	56.40	0.0003	0.0046	0.2821	0.0223	8.10	–	–	–	–	–	–	–	–	–	51.5	12
19	St Annes Lagoon	42.46	173.16	33	17.1	0.200	1.00	0.245	340.50	0.0088	1.9701	2.7099	2.8038	7.30	65.472	19.094	46.377	20.329	9.734	43.640	4.362	48.618	11.678	95	6
20	Mill	42.55	172.55	146	16.6	0.060	2.70	0.500	256.00	0.0075	0.0214	1.5481	0.1737	9.80	34.085	10.171	23.914	16.332	5.631	24.340	1.937	29.748	20.932	76	8
21	Lake Greta	42.57	172.58	183	16.3	0.020	3.10	0.440	173.60	0.2440	0.0110	1.3000	0.1140	8.90	22.581	12.140	10.442	11.441	5.192	20.709	2.732	14.542	12.176	17	4
22	Glen	43.01	172.47	78	16.8	0.070	1.40	0.177	381.00	0.0058	0.0095	3.9306	0.2077	41.30	55.731	18.358	37.373	24.575	11.255	41.668	4.741	45.233	35.606	534	13
23	Hut	43.02	172.46	71	16.9	0.100	5.00	0.195	251.00	0.1161	0.4424	2.3297	0.7642	4.40	50.101	18.875	31.226	29.642	4.323	19.202	5.144	16.923	8.784	70	5
24	Lake Pearson	43.06	171.46	611	14.6	1.790	15.00	4.450	44.90	0.0018	0.0018	0.1954	0.0072	2.36	–	–	–	–	–	–	–	–	–	156	8
25	Mystery Tarn	43.12	171.34	854	13.3	0.020	8.00	3.800	6.90	0.0061	0.0058	0.3258	0.0306	0.40	7.202	0.557	6.645	0.386	0.139	1.228	0.218	1.637	0.326	425	16

Table 1 continued

Lake Nr	Location	Lat (°S)	Long (°E)	Altitude (m)	Feb mean (°C)	Lake area (km^2)	Depth (m)	Secchi depth (m)	Cond ($\mu S\ cm^{-1}$)	NO$_x$-N (mg/l)	React P (mg/l)	TN (mg/l)	TP (mg/l)	Chl *a* ($\mu g/l$)	TC (mg/l)	DIC (mg/l)	DOC (mg/l)	Ca (mg/l)	Mg (mg/l)	Na (mg/l)	K (mg/l)	Cl (mg/l)	SO_4 (mg/l)	HC count	# Taxa
26	Lake Evelyn	43.15	171.32	580	14.7	0.150	3.00	3.000	55.80	0.0060	0.0038	0.2259	0.0278	0.60	10.917	6.024	4.893	8.391	1.342	3.129	0.258	1.058	3.001	208	12
27	Lake Heron	43.29	171.10	691	13.7	6.300	36.00	5.600	51.10	0.0148	0.0002	0.1441	0.0046	0.95	–	–	–	–	–	-	–	–	–	64	7
28	Lake Camp	43.36	171.03	674	13.8	0.490	13.00	2.100	69.60	0.0041	0.0064	0.3290	0.0338	0.50	14.058	7.492	6.567	8.495	1.500	3.481	0.393	1.289	0.794	114	12
29	Lake Roundabout	43.37	171.05	653	13.9	0.130	0.74	0.740	57.90	0.0041	0.0220	0.7061	0.1129	1.20	14.028	4.590	9.438	7.315	2.111	4.267	0.213	2.900	1.128	63.5	8
30	Lake Emma	43.38	171.06	655.5	13.9	1.550	2.20	0.720	64.10	0.0048	0.0090	0.7253	0.0608	2.10	20.686	8.737	11.949	9.406	2.242	5.120	0.323	1.674	1.528	131.5	12
31	Groynes	43.27	172.36	25	16.8	0.018	1.25	1.250	62.40	0.0065	0.0043	0.3089	0.0445	2.50	10.818	5.500	5.318	8.322	1.057	3.321	0.585	2.128	4.857	120	6
32	Lake Forsyth	43.48	172.44	20	17	5.620	1.60	0.660	1180.00	0.0806	0.0090	2.5000	0.5500	181.00	–	–	–	–	–	–	–	–	–	30	1
33	Lake Middleton	44.16	169.50	526	15.5	0.230	4.50	2.300	21.80	0.0040	0.0069	0.4094	0.0100	0.60	10.270	3.049	7.220	3.663	0.742	2.240	0.223	1.082	0.581	173.5	8
34	Red Lagoon	44.18	169.52	589	15.2	0.160	1.25	1.200	37.60	0.0042	0.0056	0.5834	0.0372	0.15	11.521	1.987	9.535	3.285	0.740	3.094	0.171	1.209	0.381	150	21
35	Swan Lagoon	44.18	169.55	576	15.2	0.345	1.40	0.660	95.30	0.0054	0.0030	3.7637	0.0100	1.50	64.716	4.993	59.723	5.127	1.954	11.841	3.193	6.081	0.200	65	7
36	Avon	44.23	169.38	734	14.4	0.100	1.50	1.400	68.30	0.0040	0.0036	0.5083	0.0481	0.60	13.952	4.312	9.640	6.467	0.985	3.294	0.157	1.230	1.874	89	12
37	Lake Sylvan	44.42	168.19	383	14.3	0.720	19.15	3.800	45.00	0.0040	0.0043	0.1818	0.0322	0.50	7.771	1.752	6.019	5.334	0.569	1.516	0.348	1.623	2.254	88	18
38	Lake Harris	44.43	168.10	1231	9.6	0.250	40.00	8.000	16.13	0.0040	0.0297	0.1699	0.0100	0.15	3.571	2.275	1.296	2.562	0.109	0.551	0.077	0.951	0.524	112	19
39	Lake Mackenzie	44.45	168.10	885.5	11.4	0.200	34.20	11.500	15.52	0.0040	0.0280	0.0100	0.0310	0.15	1.033	0.282	0.750	0.612	0.059	0.222	0.135	0.778	0.316	156.5	14
40	Gertrude Saddle	44.44	168.01	1371.5	8.4	0.010	2.90	2.900	68.20	0.0040	0.0322	0.0989	0.0253	0.15	1.284	0.145	1.139	0.133	0.066	0.330	0.035	4.093	0.217	199	19
41	Lake Howden	44.49	168.08	684	12.4	0.100	9.40	2.500	102.00	0.0040	0.0292	0.1151	0.0100	0.20	14.309	10.087	4.222	22.230	0.333	1.327	0.148	1.336	2.832	255.5	19
42	Lake Hayes	44.58	168.48	329	15.8	2.030	31.00	4.750	141.46	0.0005	0.0028	0.2400	0.0100	1.99	–	–	–	–	–	–	–	–	–	50	12
43	Lake Johnson	45.00	168.43	406	15.4	0.200	28.30	1.940	216.00	0.0040	0.0067	0.7069	0.0100	0.40	34.450	14.547	19.902	26.443	2.784	5.113	2.300	4.336	7.120	27	7
44	‘‘Sugarbowl Tarn’’	45.03	168.49	1799.5	8.2	0.014	6.15	6.200	24.30	0.0040	0.0049	0.0936	0.0263	0.20	3.971	1.486	2.485	4.126	0.222	0.298	0.139	0.766	2.066	195	4
45	Lake Alta	45.04	168.48	1882	8.2	0.130	36.10	9.850	15.38	0.0040	0.0052	0.0920	0.0246	0.15	2.058	1.139	0.919	1.645	0.133	0.498	0.086	0.811	1.001	72.5	5
46	Lake Mistletoe	45.12	167.49	207	14.6	0.100	13.65	3.500	57.70	0.0040	0.0299	0.1494	0.0274	1.10	11.159	6.741	4.417	0.881	0.376	0.318	0.097	0.777	0.350	52.5	18

Global positioning was used to determine the latitude, longitude, and altitude. Abbreviations used for physical measurements and water chemistry parameters are listed in the body of the text

water chemistry for the lakes sampled in 2002/2003 were a product of a diatom training set developed by Reid (2005).

Prior knowledge of the trophic status of potential lakes was obtained from local government monitoring records (e.g. Christchurch Regional Council, unpublished dataset), data obtained from previous studies on New Zealand aquatic ecosystems (e.g. Stout 1985; Timms 1982, 1983) and the previous investigations of New Zealand chironomid ecology by Schakau (1993) and Boubee (1983).

Small (median 0.180 km^2), shallow (median 10.2 m depth) lakes were preferentially sampled to ensure a close relationship between bottom-water temperature and air temperature. Ideally, the sampling of deep (>30 m) lakes should be avoided to eliminate the effect of hypolimnetic anoxia on the chironomid species assemblages (Little and Smol 2001). All efforts were made to select such lakes, but due to the lack of bathymetric data for New Zealand's high altitude lakes, some of the high altitude lakes selected for sampling were found to be deep (Table 1). A preliminary ordination of the species and environmental data indicated that depth was not a significant ($P < 0.05$) driver of species variation in the training set, even when these deep lakes were included.

At each lake, maximum depth was located using bathymetric maps and a NorCross Hawkeye® DF2200PX portable depth finder. When bathymetric maps were not available, multiple transects were used to determine the deepest point of the lake. At the deepest point, two surface water samples (0–1 m) were collected in acid-washed 500 ml Nalgene bottles, which were rinsed with lake water. Surface water temperature, pH, and conductivity (Cond) were measured using a Hannah® HI 8424 pH meter and thermometer, and a Eutech® Cyberscan Con 20 conductivity meter. One of the surface water samples was immediately filtered using a syringe and Whatman® 25 mm Ø GF/F glass microfibre filters. Filters were wrapped in foil and kept for subsequent analysis for Chlorophyll *a* (Chl *a*) concentration determination, which was conducted in the Environment Canterbury laboratory in Christchurch, New Zealand. The 500 ml filtered and unfiltered samples were kept frozen until analysis at the Environment Chemistry Laboratory, Massey University, Palmerston North, New Zealand. Samples were analysed for ionic concentration (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, SO_4^{2-}) and nutrients (reactive nitrogen (NO_x), reactive phosphorus (RP), total nitrogen (TN), total phosphorus (TP)), dissolved organic carbon (DOC), dissolved inorganic carbon (DIC) and total carbon (TC). Water samples collected by Michael Reid in 2002/2003 (Reid 2005) were only analysed for nutrients (NO_x, RP, TN, TP) and Chl *a*. Even though other studies have shown that oxygen concentrations may have an influence on chironomid distribution (e.g. Little and Smol 2001), dissolved oxygen was not measured during this study. A summary of the physical measurements and chemistry of water samples from each lake is presented in Table 1.

Sediment cores were taken using a Glew Mini Corer (Glew 1991) at the deepest point in each lake. Where the main basin was large, or there was more than one sub-basin, several sites were sampled and the samples combined later to form a composite sample. The top 2 cm of each core were extruded while still in the boat, sampled at 1 cm intervals and placed in Whirl-paks®. Sediment samples were kept cool and out of direct sunlight until they could be processed.

Even though measurements for surface water temperature were taken in the field, the February mean (late austral summer) air temperature was used as the temperature variable in all numerical analyses. Chironomid assemblages are likely to be influenced by both air temperature (e.g., during pupation, flight, reproduction and dispersal (Hoffman 1986; Walker and Mathewes 1989)) and water temperature (e.g., larval development rates and mortality (Robb 1966)). Walker et al. (1991) and Olander et al. (1997) have demonstrated that there is a close relationship between air and water temperature for shallow polymictic lakes. Therefore, in the absence of long-term water temperature measurements, the use of mean monthly climate data is appropriate. February mean temperature measurements were extracted from a climate surface fitted to data from 346 weather stations covering a period of 30 years (Leathwick et al. 1998).

Sample preparation for chironomid analysis

Sediment samples were processed for chironomids following a modified version of the method outlined in Hofmann (1986). Samples were weighed, deflocculated in hot 10% KOH and washed on a 93-μm mesh with copious amounts of distilled water. Samples were then transferred to a Bogorov counting tray and examined for invertebrate remains under a dissection microscope, at 50× magnification. An average of 10 ml of wet sediment was required to achieve the target head-capsule quantity. A corresponding 2 ml sub-sample of un-processed sediment was dried at 50°C for 3 days for the purpose of chironomid head-capsule concentration calculations.

Chironomid head-capsules were mounted on glass slides in a drop of lactophenol PVA and covered with a glass coverslip. Head-capsules were mounted ventral side up to facilitate identification. Chironomids were identified using a transmission light microscope with the aid of publications by Forsyth (1971), Boubee (1983), Schakau (1993) and identification guides by Boothroyd (1994, 1999, 2002).

Statistical methods

Constrained and unconstrained ordinations were performed using CANOCO version 4.5 (ter Braak and Šmilauer 2002) to explore the relationships between modern chironomid assemblages and environmental variables, as well as to screen environmental and species data for outliers.

Secchi depth measurements were removed from the original environmental dataset as the secchi depth was potentially greater than the lake depth (i.e. the disc was visible on the bottom) in six lakes (Table 1). Latitude, longitude, altitude, and lake area values were also removed from the environmental dataset. These parameters indirectly affect chironomid distribution (i.e., they affect such factors as temperature and productivity) but are unlikely to have a direct effect on chironomid distribution.

In removing latitude and longitude it was assumed that the distribution of New Zealand chironomids is controlled by environmental tolerance and that biogeography plays only a minor role on the scale represented in this study. This hypothesis was confirmed by performing partial canonical correspondence analyses (CCA) in CANOCO 4.5 (ter Braak and Šmilauer 2002) constrained to latitude and longitude respectively (both parameters untransformed). Only longitude displayed a significant ($P \leq 0.05$) relationship to chironomid distribution. It was suspected that this was due to the prevalence of highly productive lakes on the lowlands to the east of the Southern Alps (Fig. 1). This was confirmed by partialling out the effect of Chl *a*, which reduced the significance (P) of longitude from 0.001 to 0.222 and the explanatory power (λ_1/λ_2) from 0.583 to 0.258.

The remaining 18 environmental variables were tested for normality using SPSS® statistical software (SPSS Inc. 2002). Log_{10} transformations were required to normalise all environmental data except for depth, February mean, and pH.

Two separate groups of analyses were performed based on the availability of environmental data. The first group of analyses (hereafter referred to as the non-ion data set) was performed using a dataset containing all 46 lakes. This group of analyses tested the explanatory power of the 9 environmental variables (depth, February mean, Cond, pH, NO_x, RP, TN, TP, and Chl *a*) available for all of the lakes (Table 1). The second group of analyses (hereafter referred to as the ion dataset) focused on a sub-set of 33 lakes for which data on all 18 environmental parameters (depth, February mean, conductivity, pH, NO_x, RP, TN, TP, Chl *a*, TC, DIC, DOC, Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, Cl^{-}, and SO_4^{2-}) were available (Table 1).

Chironomid species data were used in the form of square root transformed percentage data (%) and log transformed (log (x+1)) concentration data (head-capsules/g dry sediment). All analyses were performed separately using datasets containing either: all taxa (concentration and % data), taxa with abundances ≥2% in at least 2 lakes (% data only), or taxa with $N2$ values ≥2 (concentration and % data).

All samples were removed from the dataset if the chironomid head-capsule count was less than 50. Quinlan and Smol (2001) argue that a minimum count of 40–50 head-capsules is sufficient for use in inference models where diversity is low.

Rarefaction analysis (see Fig. 2) of the species data (Birks and Line 1992) revealed that a sample size of at least 50 head-capsules captured an average of 80% of the actual taxonomic richness in the New Zealand chironomid assemblages. A regression of taxonomic richness vs. total head-capsule count (Fig. 2) revealed a low correlation ($r^2 = 0.2253$) between the sample size and taxonomic richness.

Unconstrained ordinations (principle components analysis (PCA), and detrended correspondence analysis (DCA)) were used to identify outliers in the training set and explore the patterns of compositional variation and biological species turnover (the gradient length). Partial, constrained ordinations (redundancy analysis (RDA), CCA) were used to determine which environmental variables were highly correlated to chironomid distribution. The statistical significance of each environmental variable was tested by Monte Carlo permutation test (999 unrestricted permutations under the full model). Variables with a significant ($P \leq 0.05$) were retained for further analyses. The unique explanatory power of each significant environmental variable was tested using a series of partial, constrained ordinations (RDA or CCA) with all other significant environmental parameters as co-variables. Only environmental parameters that retained their significance after these analyses were considered for transfer function development.

Quantitative transfer functions for the significant environmental variables selected in the CCAs and RDAs were developed in the computer program C2 (Juggins 2003). Gradient lengths for the first axis in a detrended canonical correspondence analysis (DCCA) constrained to a single environmental parameter were used to decide between linear (partial least squares (PLS)) or unimodal (weighted averaging (WA) and weighted averaging-partial least squares (WA-PLS)) models (Birks 1995, 1998).

Robust transfer functions were those that had a low root mean squared error of prediction (RMSEP), a high coefficient of determination (r^2_{jack}) and a low mean and maximum bias (Birks 1998).

Results and discussion

Data screening

Fifty chironomid taxa were identified and enumerated from the 46 lake training set (Appendix Table 4). Only 3 lakes failed to produce sufficient head-capsules (≥50; Lakes 21, 32, and 43: see Table 1). These lakes were excluded from further

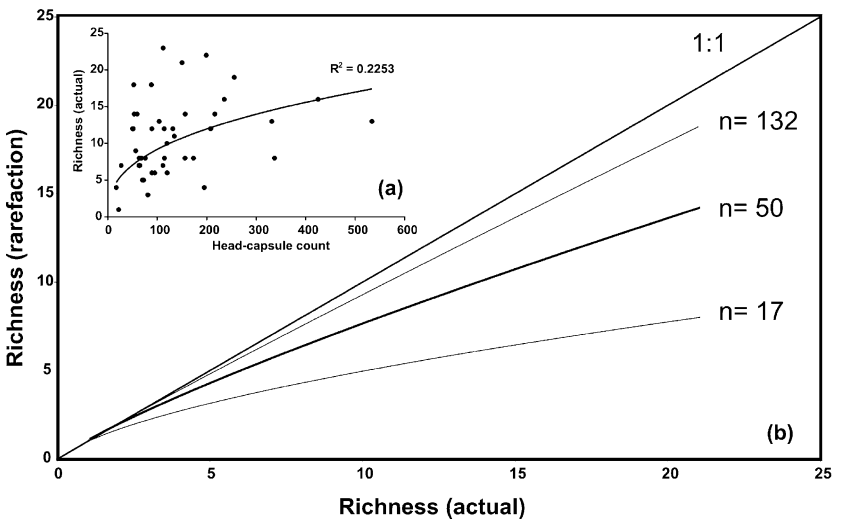

Fig. 2 Taxon richness in subfossil chironomid samples from New Zealand. (**a**) Relationship between total number of head-capsules and actual sample richness. (**b**) Comparison of richness before and after rarefaction analyses calculated for head-capsule numbers (n) = 17 (lowest count), 50 (accepted minimum count for inclusion of a lake) and 132 (mean number of head-capsules counted for each lake)

analyses. Analyses were performed using both percentage data (%) and concentration data (head-capsules/g dry sediment) for the larger (46 lake) dataset, and the smaller (33 lake) subset using all species datasets (all species, ≥2% and $N2 \geq 2$). Species percentage data outperformed species head-capsule concentration data in all cases. Concentration data also failed to produce any unique species/environment relationships.

The retention of all of the species in the analyses reduced the performance (significance (*P* value) and λ_1/λ_2) of environmental variables in partial constrained ordinations with and without co-variables; possibly due to the introduction of noise provided by rare taxa. Therefore, the following discussion will focus on the results from species percentage data (≥2% and $N2 \geq 2$) ordinations.

A PCA of the ion dataset indicated that there was a great deal of redundancy (i.e., colinearity). It was expected that the addition of the ionic data would not provide any extra relationships over those provided by the reduced dataset. A series of ordinations was used to test this theory. A CCA was performed using the ion set environmental parameters with species percentage data. Variables with high variance inflation factors (>20), (TC, Mg^{2+}, DOC, and Na^{+}), were removed one at a time starting with the largest value (TC) until all values were <20 (ter Braak and Šmilauer 1998). Out of the remaining 14 environmental variables only temperature (February mean) retained a significant relationship to chironomid species composition after partial, constrained ordinations with co-variables. Temperature (February mean) also emerged as the strongest predictor of chironomid species composition in the non-ion dataset. Therefore further statistical analyses focused on this dataset.

A PCA of the environmental data and a DCA of the chironomid data (≥2% and $N2 \geq 2$ deletion criteria) were performed for the non-ion dataset. Samples whose scores for axes 1 and 2 were outside one standard deviation (SD) of the mean for both axes in both the PCA and DCA (for environmental and species data, respectively) were considered outliers and were removed from further statistical analysis. Lakes 19 and 23 were identified as outliers in the PCA due to extreme values of area, TP, and RP, respectively. Both of these lakes are shallow, eutrophic, and located in catchments that are severely modified by human activities. Lake 1 was also removed from the dataset. Even though area was not considered as an environmental variable for reconstruction, the large size (79.78 km^2) and moderate depth (20.5 m) of this lake will quite likely result in a chironomid assemblage that is almost entirely dominated by profundal species in a sample taken from the lake centre.

No outliers were identified in a DCA using the smaller (≥2% deletion criterion) species dataset, but 3 lakes (40, 45, and 46) were identified as outliers in the DCA based on the larger ($N2 \geq 2$) species dataset. Lake 40 was an acidic (pH 5.3) high altitude (1371 m) lake with a high percentage (~22%) of head-capsules from *Parochlus*. Lake 45 was a deep (36.1 m) high altitude (1882 m) lake with high percentages of *Naonella forsythi* and *Tanytarsus vespertinus* (~11% and 30%, respectively). Both *Parochlus* and *Naonella forsythi* are common in cold, fast flowing streams and rivers (Brundin 1967; Taylor 2001). It is possible that where conditions in the lake are unfavourable (cold, deep, acidic) the contribution of river-borne head-capsules may be high. Lake 46 had a diverse (18 taxa) chironomid fauna. There were numerous species present in this lake that were rare (<2% relative abundance) elsewhere in the training set. This lake was highly stained (with high concentrations of dissolved tannic and humic substances) and situated in a forested catchment. Schakau (1993) found that species diversity (Shannon Weaver Index *H′*) was highest in lakes in heavily forested catchments.

The main environmental controls on New Zealand chironomid species

A series of ordinations were performed on the screened data to determine which environmental parameter(s) exerted the strongest influence on chironomid distribution in New Zealand. A DCA with detrending-by-segments was performed on both species datasets (≥2% and $N2 \geq 2$) to determine the most appropriate constrained ordination method. The results of the DCA for both datasets were similar. Axes 1 and 2 for each

analysis had eigenvalues of 0.270 and 0.135 (≥2% species dataset), and 0.294 and 0.147 ($N2 \geq 2$ species dataset). Axis 1 in the ≥2% species dataset accounted for 20% of the total variation in the chironomid dataset, compared to 18.2% for the $N2 \geq 2$ species dataset. Gradient lengths for Axis 1 were 2.901 SD for the ≥2% species dataset and 3.003 SD for the $N2 \geq 2$ species dataset. Gradient-length values <2 SD suggest the use of RDA while those >4 SD suggest the use of CCA (ter Braak 1995). Results for a CCA and a RDA were examined for both species datasets as the gradient lengths fall between the cut-off values suggested by ter Braak (1995). In both cases the CCA explained a higher percentage of the total species variation; therefore all further ordinations were performed using this method.

CCAs constrained to each of the 8 environmental variables for each species dataset identified February mean, Cond, TN, and Chl *a* as significant ($P \leq 0.05$) explanatory environmental variables for both species datasets (≥2% and $N2 \geq 2$), while CCAs on the ≥2% species dataset also extracted pH as a significant explanatory environmental variable for species distribution (Table 2, Fig. 3). In both cases (≥2% and $N2 \geq 2$) February mean explained the greatest significant amount of variation in the chironomid species data (13.6% and 10.6%, respectively), followed by Chl *a* (8.5% and 8.4%, respectively) and Cond (7.8% and 7.5%, respectively).

CCAs constrained to all significant environmental variables at once for both species datasets returned similar results (Table 3). A CCA of the ≥2% species data constrained to the 5 environmental parameters (February mean, Cond, TN, Chl *a*, and pH) explained slightly more of the variation in the chironomid species data (25.1% for 4 axes) than the $N2 \geq 2$ species dataset constrained to 4 environmental variables (21.1% for 4 axes). In both cases February mean was significantly correlated to CCA axes 1 and 2 (Table 3). The eigenvalue for axis 1 was high for both CCAs (0.169 and 0.160, respectively), and axis 1 explained >50% of the total variance of the species–environment relation in both cases.

Partial CCAs constrained to each variable, by itself, and with other significant environmental

Table 2 Results of a partial CCA for the significant ($P < 0.05$) environmental variables by themselves and with the effects of other variables partialled out

Environmental		≥2% deletion criterion				$N2 \geq 2$ deletion criterion			
Variable	Covariable(s)	λ_1	λ_1/λ_2	P	% variance	λ_1	λ_1/λ_2	P	% variance
Feb mean	None	0.173	0.935	0.001	13.6	0.106	0.488	0.001	10.6
	Cond	0.118	0.670	0.001	10.1	0.091	0.520	0.004	6.7
	TN	0.106	0.596	0.001	9	0.097	0.567	0.001	7
	Chl *a*	0.115	0.622	0.001	9.9	0.112	0.626	0.001	8.3
	TN, Cond, Chl *a*	0.103	0.640	0.001	9.2	0.081	0.482	0.002	6.4
	pH	0.157	0.853	0.001	12.9	–	–	–	–
	TN, Cond, Chl *a*, pH	0.096	0.568	0.001	9	–	–	–	–
Cond	None	0.099	0.442	0.001	7.8	0.075	0.333	0.004	7.5
	Feb mean	0.045	0.256	0.08	4.1	0.045	0.257	0.228	3.4
TN	None	0.094	0.152	0.002	7.4	0.065	0.289	0.01	6.5
	Feb mean	0.027	0.159	0.549	2.4	0.031	0.181	0.686	2.3
Chl *a*	None	0.109	0.537	0.001	8.5	0.126	0.609	0.001	8.4
	Feb mean	0.051	0.276	0.048	4.6	0.088	0.486	0.001	6.5
	Cond	0.062	0.312	0.02	5.3	0.06	0.324	0.032	4.4
	TN	0.048	0.249	0.09	4.3	0.076	0.388	0.005	5.4
	TN, Cond, Feb mean	0.047	0.297	0.058	5.2	0.059	0.351	0.049	4.8
	pH	0.092	0.465	0.001	7.6	–	–	–	–
pH	None	0.058	0.236	0.041	4.6	–	–	–	–
	Feb mean	0.043	0.234	0.114	3.9	–	–	–	–

The eigen value of the first CCA axis (λ_1), the ratio of the eigen value for axes 1 and 2 (λ_1/λ_2), the statistical significance (P), and the percentage of variance of the species data (% variance) are shown for both the smaller (≥2 in at least 2 lakes) and larger ($N2 \geq 2$) species datasets (left column and right column, respectively)

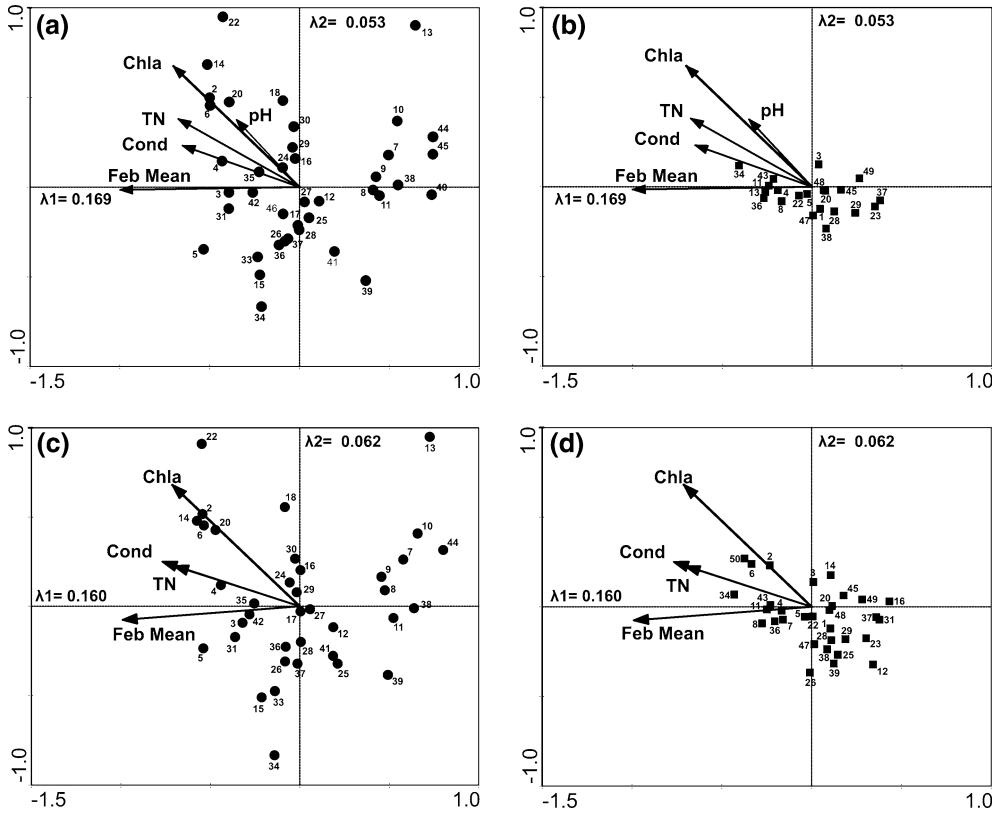

Fig. 3 CCA biplots for axis 1 vs. axis 2 (λ_1 vs. λ_2). Environmental variables (*arrows*) are shown. Chl *a*, TN, Cond, Feb mean and pH. Lake numbers (*points*) and species numbers (*squares*) correspond to Table 1 and Appendix A, respectively. (**a**) and (**b**) Partial CCA of sites and species respectively for the smaller (>2%) species dataset. (**c**) and (**d**) Partial CCA of sites and species respectively for the larger ($N2 \geq 2$) species dataset

parameters as co-variables were then performed to test the explanatory power of each individual variable (Table 2). Quantitative inference models (transfer functions) would only be attempted for environmental parameters that explained a significant proportion of the variation in the species data, both individually and when the effects of each of the other environmental variables were partialled out.

Analyses were run on both sets of species data (≥2% and $N2 \geq 2$) as Chl *a* seemed to perform slightly better with the larger species dataset. Chl *a* was significantly correlated to axis 2 in both CCAs constrained to all the environmental variables. However, the larger species dataset increased the canonical regression co-efficient and the significance as calculated by an approximate *t*-value (Table 3).

February mean was the only environmental variable to remain significant ($P \leq 0.05$) in a set of partial CCAs with other variables entered as co-variables for the ≥2% species dataset (Table 2). February mean remained significant ($P = 0.001$) and explained ≥9% of the variation in the chironomid species data after the removal of the effects of all of the other significant ($P \leq 0.05$) environmental variables separately and combined. Chl *a* was the only other environmental variable to remain significant ($P \leq 0.05$) after the effect of temperature was partialled out. However, the explanatory power of this variable was reduced after the effect of TN and the combined effect of February mean, Cond, and TN were partialled out (Table 2).

February mean remained the most significant environmental variable in a series of partial CCAs using the $N2 \geq 2$ species data, but did not perform quite as well as it did with the other species dataset (Table 2). The species–environment relationship remained significant ($P \leq 0.05$)

Table 3 Canonical co-efficients, *t*-values, and CCA summary from a partial CCA including all significant ($P < 0.05$) environmental variables for the smaller (≥2% in at least 2 lakes) and larger ($N2 \geq 2$) species datasets (left column and right column, respectively)

Axis:	Species deletion criteria							
	≥2%				*N*2 ≥2			
	AX1	AX2	AX3	AX4	AX1	AX2	AX3	AX4
Regression/canonical co-efficients								
Eigen value	0.169	0.053	0.044	0.035	0.160	0.062	0.027	0.019
Cum. % var. spp.	14.1	18.5	22.2	25.1	12.5	17.4	19.6	21.1
Variable								
Feb mean	−0.999	−1.079	−0.486	−0.195	−0.829	−1.081	0.607	0.564
Cond	0.026	0.015	1.210	0.735	−0.144	0.131	−1.454	0.052
TN	−0.076	0.298	0.129	−0.197	−0.088	0.094	0.184	−1.350
Chl *a*	0.043	1.226	−0.180	−0.603	−0.010	1.270	0.542	0.495
pH	0.007	0.096	−0.772	0.843	–	–	–	–
t-*values for regression co-efficients*								
FR explained	0.534	0.169	0.140	0.112	0.596	0.232	0.101	0.072
Variable								
Feb mean	−5.504	−3.999	−1.462	−0.577	−4.548	−4.641	1.940	1.014
Cond	0.160	0.061	4.077	2.432	−0.857	0.612	−5.044	0.101
TN	−0.450	1.193	0.419	−0.631	−0.564	0.468	0.684	−2.829
Chl *a*	0.248	4.783	−0.570	−1.877	−0.060	5.927	1.882	0.967
pH	0.051	0.484	−3.150	3.380	–	–	–	–

Eigenvalues are shown for the first 4 axes (AX1, AX2, AX3 and AX4) along with the cumulative % of variance in the species data explained by each axes (Cum. % var. spp.)

but the amount of variance this variable explained in the species data was reduced by the partialling out of the effect of Cond from 10.6% to 6.7%. Chl *a* performed slightly better in a series of partial CCAs using the $N2 \geq 2$ species dataset (Table 2). Chl *a* remained significant ($P \leq 0.05$) when the individual and combined effects of the other significant environmental variables were partialled out. The partialling out of the effect of Cond had the greatest detrimental effect on the explanatory power of Chl *a*. Partialling out the effects of conductivity reduced the amount of variance Chl *a* explained in the species data from 8.4% to 4.4% and reduced the statistical significance (P) from 0.001 to 0.032.

Chironomid species responses to the main environmental parameters

Temperature

New Zealand subfossil chironomid assemblages showed marked changes in species composition corresponding to gradients of altitude and temperature (Fig. 4). Six main zones of faunistic turnover (based on all 50 taxa) were returned in a zone analysis using the CONISS function in Zone 1.2 (Juggins 1992). The main zone of faunistic change approximated the tree-line (~1000–1300 m). Other workers (e.g. Porinchu and Cwynar 2000) have identified the tree-line as an important ecological boundary controlling chironomid distribution. *Cladopelma curtivalva*, *Cricotopus zealandicus*, *Cricotopus aucklandensis*, and *Polypedilum* were characteristic of warm (>13°C) temperatures. These genera (particularly *C. curtivalva* and *Polypedilum*) are also typical of warmer conditions in other parts of the world (Walker et al. 1991; Larocque et al. 2001). *Naonella kimihia* was also somewhat restricted to lower altitudes but remained as a component of the chironomid fauna at altitudes extending somewhat above the tree-line (~1300 m). The high altitude fauna (>1300 m) were dominated by 5 taxa; 4 species of Chironominae (*Chironomus*, *Corynocera*, *Tanytarsus funebris*, and *Tanytarsus vespertinus*) and head-capsules belonging to the tribe Macropelopiini. All of these species are also

present in high abundances in lowland lakes (Fig. 4). It appears that these species have a wide tolerance for temperature, but only occur in abundance below the tree-line in oligotrophic to mesotrophic lakes (with the exception of *Chironomus*) (Fig. 5). Brodersen et al. (2004) found that cold-water assemblages in low-arctic West Greenland were dominated by oxy-conformers; chironomids incapable of surviving low concentrations of dissolved oxygen. All the main high altitude species (except *Chironomus*), were rare or absent in eutrophic lowland lakes (Fig. 5); suggesting that this is also the case for the New Zealand fauna. The genus *Chironomus*, on the other hand, was also present in high concentrations in eutrophic lowland lakes.

Robb (1966) found that *Chironomus zealandicus* had a wide tolerance for extreme values for a large number of environmental gradients (e.g. temperature, pH, conductivity, and dissolved oxygen). So it could be that *Chironomus zealandicus* is the dominant *Chironomus* species represented in this training set and it becomes more common when conditions are outside the tolerance of other chironomid species. It could also be the case that the *Chironomus* morphotype represents more than one species in this training set. Preliminary work involving the integration of morphological, ecological and karyotypic studies (Assoc. Prof. Jon Martin and Don Forsyth unpublished data) suggests the existence of up to nine distinct *Chironomus* species on the New Zealand mainland. Future work should focus on relating easily identifiable features on the head-capsule to each of the nine karyotypes. Further attention to resolving the taxonomy of the Macropelopiini in New Zealand is also required. At present there is no consensus on the taxonomy of the larval stages (e.g. Schakau 1993; Stark 1981). The potential for the use of cephalic setation (see Rieradevall and Brooks 2001) was investigated briefly during the course of this study, but requires further work.

Species typical of rhithral (upland) streams (Orthocladiinae, Podonominae, and Diamesinae) were also common but not usually very abundant in high altitude lakes. Rhithral stream species are dominated by cold stenotherms (Burgherr and Ward 2001) so it is not surprising that these contribute to the chironomid fauna found in high altitude lakes.

Chlorophyll a

The distribution of the main (≥2% mean abundance) chironomid species with respect to the concentration of Chl *a* is shown in Fig. 5. The statistical significance of various models was tested in CANOCO 4.5 (ter Braak and Šmilauer 2002) for their ability to explain the distribution

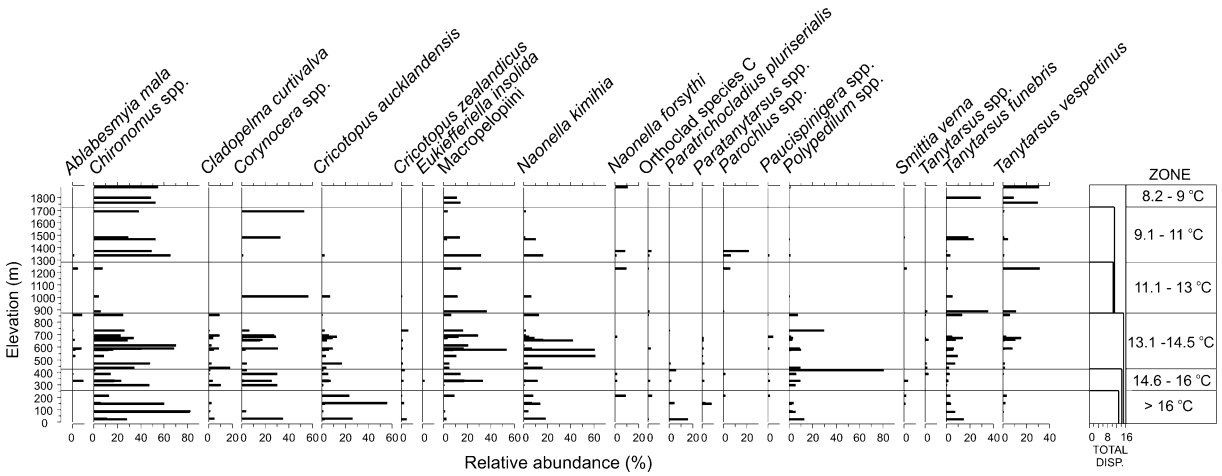

Fig. 4 Distribution and percentages of the main New Zealand chironomid species along an altitudinal gradient. All taxa present ≥2% in at least 2 lakes are shown. Lakes are ordered according to their elevations (m a.s.l.) and corresponding zones of mean February temperature are indicated

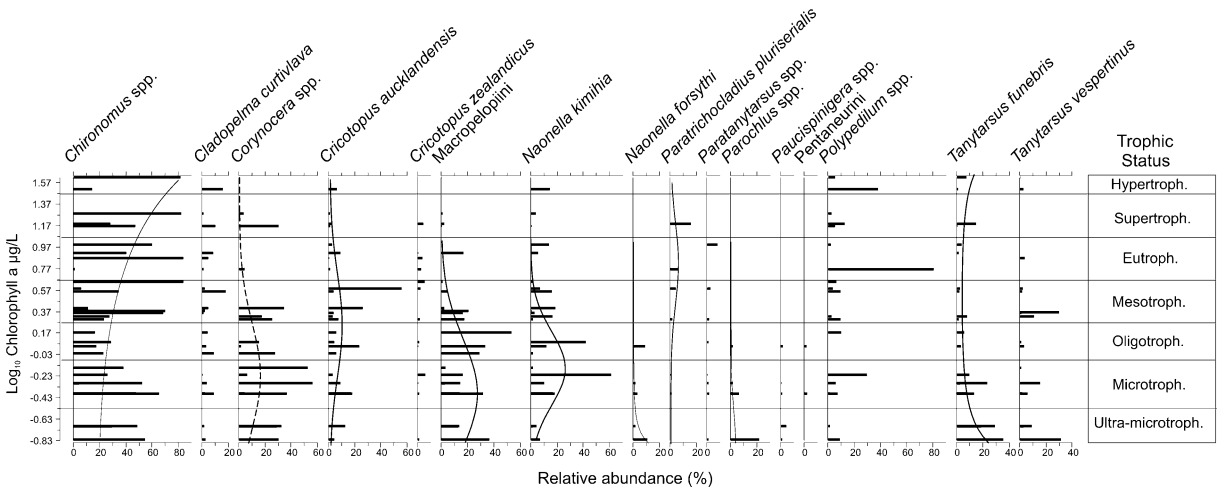

Fig. 5 Distribution and percentages of the main New Zealand chironomid species along a gradient of trophic status (Chl *a* concentration). Trophic classifications based on Burns et al. (2000). Solid curves are fitted significant ($P < 0.05$) models developed in CANOCO 4.5 (ter Braak and Šmilauer 2002). Dashed curve is less significant ($P = 0.09$)

of each of the main chironomid taxa with respect to Chl *a*. All of the curves plotted in Fig. 5 were significant ($P \leq 0.05$) except for the dashed curve which represents the distribution of *Corynocera* spp. ($P = 0.09$). In all cases a quadratic Poisson distribution explained the greatest significant amount of variation in the species data. The main trend to note is that most of the common (mean abundance ≥2%) New Zealand chironomid species have wide tolerances for Chl *a*. Species assemblages (particularly in the range of ultra-microtrophic to mesotrophic) are characterised by changes in relative abundance rather than the appearance and disappearance of different species. As mentioned in the previous section, *Chironomus* is common in lakes with a wide range of productivity, but tends to dominate the chironomid assemblages in hypertrophic lakes (Fig. 5). *Chironomus* is also characteristic of highly productive lakes in other parts of the world (e.g. Brodersen and Lindegaard 1999). Once again further investigation into the taxonomy of this genus may reveal that certain *Chironomus* species are characteristic of different levels of lake production. *Polypedilum* is also tolerant of a wide Chl *a* gradient and is common in eutrophic lakes. Temperature appears to be the main limiting factor on the distribution of *Polypedilum* however, as the best model fitted to the distribution of this species with respect to Chl *a* was not statistically significant ($P = 0.18$). This hypothesis was confirmed by testing the significance of the distribution of *Polypedilum* with respect to temperature in CANOCO version 4.5 (ter Braak and Šmilauer 2002) ($P = 0.01$, quadratic Poisson distribution).

Paratrichocladius pluriserialis was the only widely occurring species limited to the mesotrophic–hypertrophic end of the scale. *P. pluriserialis* is relatively rare (mean abundance 1.14%) and is most common in lake 22, a small (0.020 km^2), shallow (3.1 m) hypertrophic pond. Species typical of the ultramicrotrophic–mesotrophic end of the Chl *a* gradient also tended to be common in high altitude lakes (see discussion in the previous section). *N. kimihia* and *Cricotopus aucklandensis* are the only common species that are abundant in ultra-microtrophic to mesotrophic lakes that are not also common above the tree-line (~1000–1300 m). *C. aucklandensis* was a more tolerant species, with a wider distribution and an optimum at the transition from oligotrophic to mesotrophic trophic status (Fig. 5). *N. kimihia* was more limited in its distribution, occurring in low abundances in highly productive lakes. The *N. kimihia* species optimum was slightly lower than *C. aucklanden-*

sis, occurring at the transition from microtrophic to oligotrophic trophic status (Fig. 5).

Model development

The ratio of λ_1/λ_2 for February mean remained large (≥0.568) and significant (P=0.001) after a series of partial CCAs (Table 2), therefore confirming that this variable explains an independent and statistically significant amount of variation in the New Zealand chironomid species data. Chl *a* did not perform quite as well as February mean; the explanatory power (λ_1/λ_2) and significance (P) of this variable was reduced by the partialling out of other environmental parameters, particularly conductivity. Chl *a* remained significant ($P \leq 0.05$) after the partialling out of conductivity, but the ratio of λ_1/λ_2 was reduced to 0.351. Even though the value of λ_1/λ_2 value for Chl *a* is low, other studies with similarly low λ_1/λ_2 values (< 0.4) have produced robust quantitative inference models for the target variable (Rosén et al. 2000; Bloom et al. 2003).

A check for sites with extreme values (>8X) for each variable (February mean and Chl *a*) as identified by the leverage diagnostic, failed to identify any sites where these environmental variables had an unduly large effect on the ordination results. Gradient lengths for the first axis in a DCCA constrained first to temperature (with the ≥2% species data) and then to Chl *a* ($N2 \geq 2$ species data) were used to determine whether to use linear (e.g. PLS) or unimodal (e.g. WA) modelling methods (Birks 1995, 1998). The gradient lengths determined by DCCA with axis 1 constrained first to temperature (gradient length = 1.533 SD) and then to Chl *a* (gradient length = 1.602 SD) suggest the use of linear (PLS) models. However, ter Braak and Juggins (1993) argue that with short gradient lengths (< 2 SD) unimodal models may outperform linear models. Therefore both unimodal (WA, WA-PLS) and linear (PLS) models were tested for each environmental variable using the computer programme C2 (Juggins 2003).

Models were accepted if they had high r^2 values, a low RMSEP, RMSEP as a % of the gradient, and a low mean and maximum bias. A minimum adequate model was selected following the criterion recommended by Birks (1998). Extra components (1, 2, 3,...,*n*) were only included in the model if the new model improved on the RMSEP of the model with 1 component by at least 5%.

Model performance

Temperature

The best temperature model (r^2=0.80, $r^2_{jack} = 0.62$, $RMSEP_{jack}$ = 1.75°C, maximum $bias_{jack}$ = 2.15°C) was developed using unimodal methods (WA-PLS with 2 components, jack-knifing) including 40 lakes (lakes 1, 19, 21, 23, 32, 43 removed) and all species with abundances ≥2% in at least 2 lakes (Fig. 6a, b). There was a slight trend in the residuals, with the model having a tendency to over predict lower temperatures and under predict higher temperatures. This tendency is regarded as an inherent feature of WA-PLS based models (ter Braak and Juggins 1993; Lotter et al. 1997).

However, the presence of *Chironomus* in high altitude lakes and low altitude eutrophic lakes may also contribute to this effect. The beta coefficient for *Chironomus* is 12.3°C, therefore in warm (>16°C), lowland, eutrophic lakes (such as lakes 6 and 22 in Fig. 6) where the observed February mean was high, the abundance of *Chironomus* (>80%) will cause an under-prediction of the temperature. The reverse is the case for high altitude lakes where *Chironomus* is abundant (e.g. lakes 40, 44, and 45 in Fig. 6a, b). Observed February mean temperatures for these lakes are < 9°C, whereas the model over predicts the temperature in each case by up to 1.5°C (Fig. 6b).

A possible criticism of this chironomid training set (as far as temperature is concerned) is the presence of two long environmental gradients i.e., temperature *and* lake production (Chl *a*). Many studies (e.g. Brooks and Birks 2000) have selected sub-sets of an originally larger training set in order to focus on only one environmental parameter (temperature in the case of Brooks and Birks 2000). Larocque et al. (2001) also state that temperature inference models are likely to be more reliable if they are developed from training

sets where the amount of human impact is minimal.

Removing highly productive lakes from a training set intended for a temperature model is usually performed to avoid problems associated with disentangling the nutrient and climate signals from the biological training set. This problem has proven controversial in this field in the past (e.g. Walker and Mathewes 1987; Warner and Hann 1987). Even though this training set contained two long environmental gradients, the results of the partial CCAs (Table 2) show that temperature was by far the strongest environmental influence on the distribution of New Zealand chironomids. This remained then case, even when the effect of Chl *a* was partialled out. Investigating long temperature and nutrient gradients in this case revealed the problematic distribution of the *Chironomus* morphotype. Had we only examined a temperature gradient

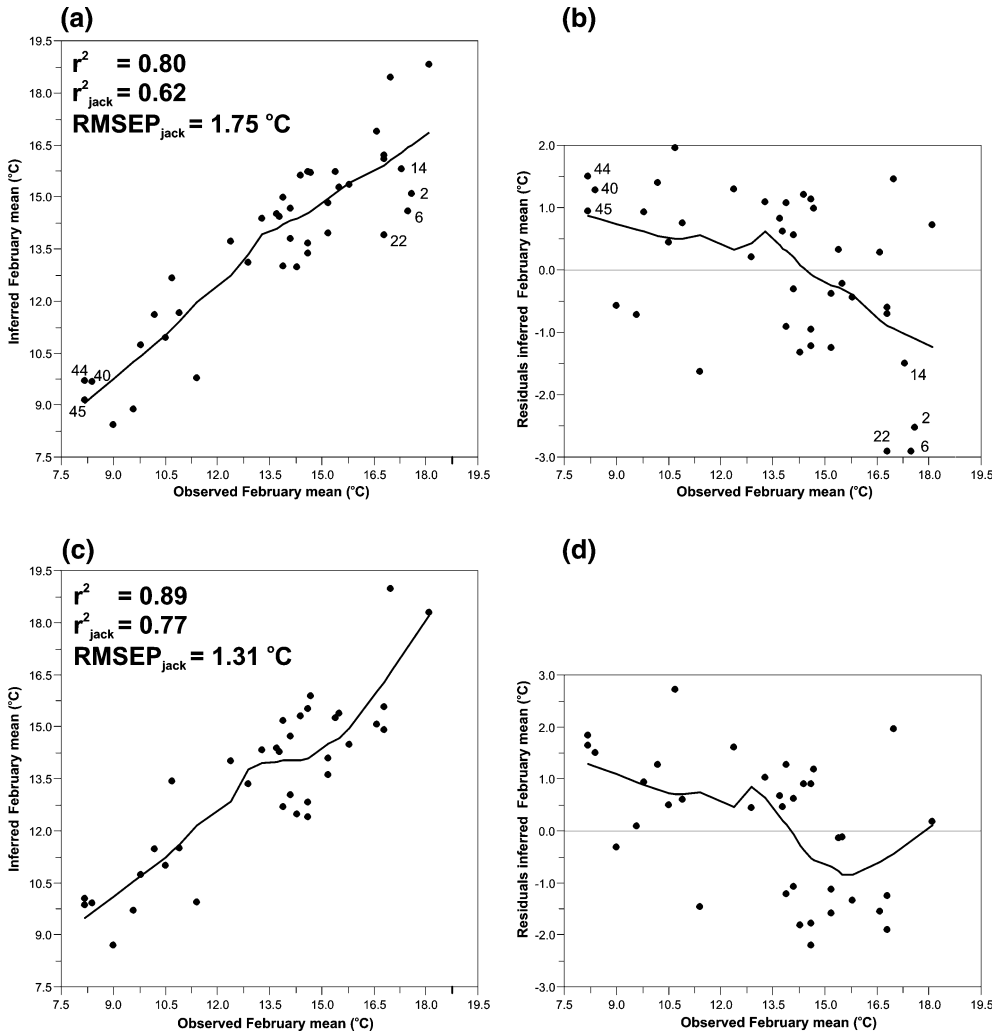

Fig. 6 (**a**) Plot of chironomid inferred February mean vs. observed February mean, and (**b**) observed vs. residual (chironomid-inferred minus observed February mean) using weighted averaging partial least squares (WA-PLS) regression. With the eutrophic lakes 2, 6, 14 and 22 included. (**c**) Plot of chironomid inferred February mean vs. observed February mean, and (**d**) observed vs. residual (chironomid-inferred minus observed February mean) using weighted averaging partial least squares (WA-PLS) regression lakes 2, 6, 14 and 22 removed. Loess smoother shown in all figures with a span of 0.45

and removed all of the highly productive lakes at the beginning, this trend would have gone un-noticed.

If we were to follow the strategy of Brooks and Birks (2000) (and others) and eliminate the highly productive (Chl *a* ≥10 μg/l) lakes from our dataset (lakes 2, 6, 14 and 22), the resulting model is far more robust (r^2 = 0.89, r^2_{jack} = 0.76, $RMSEP_{jack}$ = 1.3°C, maximum $bias_{jack}$ = 1.46°C) (Fig. 6c, d). The statistical significance (*P*) for February mean temperature in this reduced dataset was checked using a series of partial CCAs in CANOCO 4.5 (ter Braak and Šmilauer 2002) and confirmed that temperature remained significant ($P \leq 0.05$) after the partialling out of all other environmental variables. When the effect of temperature was partialled out in this reduced dataset, Chl *a* explained a relatively small (4.9%), and statistically insignificant ($P = 0.07$) amount of the total variance in the chironomid species data.

We can now say that this model would only be reliable in situations where the proportion of *Chironomus* is low, or if the proportion is high, where we could guarantee that conditions were not eutrophic or saline (Cond > 100 μS cm^{-1}). Obviously this temperature model would be unreliable when applied to brackish coastal lakes or Holocene records from lowland lakes with catchments that have experienced intensive human modification.

Highly eutrophic conditions are also possible in the absence of human impact (e.g., Brüchmann and Jörg 2004); therefore the presence of other fossils in lake sediments (e.g., *Isoetes* megaspores, charophyte oospores and the remains of other aquatic insects) could provide a guide to the past nutrient status of a particular lake. During the development of this training set it was observed that certain charophyte oospores, and *Isoetes* megaspores were absent from eutrophic, highly saline lakes. Other studies on New Zealand lakes (e.g., Stout 1985; Timms 1982, 1983) provide information on the presence or absence of particular aquatic insects in lakes of varying trophic status.

The future revision of the genus *Chironomus* may enable a differentiation between a high altitude cold stenothermic *Chironomus* species and a low altitude *Chironomus* species that is tolerant of low levels of dissolved oxygen. In the meantime this training set highlights the pitfalls of ignoring other environmental gradients, particularly nutrients in the development of a temperature inference model.

Chlorophyll a

The best model for Chl *a* (r^2 = 0.66, r^2_{jack} = 0.49, and $RMSEP_{jack}$ = 0.46 $\log_{10}$μg/l Chl *a*) was developed using linear methods (PLS with 2 components, leave-one-out cross validation) with 37 lakes (lakes 1, 19, 21, 23, 32, 40, 43, 45, and 46 removed) and all species with *N*2 values ≥2 included (Fig. 7a, b). There was a tendency for this model to under-predict the concentration of Chl *a* at the high end of the gradient (Fig. 7b).

Even though Chl *a* was shown to be a statistically significant independent driver of chironomid distribution in New Zealand (Table 2), the resulting transfer function is not particularly robust. Reid's (2005) New Zealand diatom-based Chl *a* transfer function has a lower $RMSEP_{jack}$ (0.18 Log_{10} μg/l Chl *a*) and a much higher r^2_{jack} (0.71). The only other published chironomid-based Chl *a* transfer function (Brodersen and Lindegaard 1999) also outperforms this transfer function in terms of r^2_{jack} (0.70), has a higher absolute $RMSEP_{jack}$ (0.63 Log_{10} μg/l Chl *a*), but covers a greater variation in Chl *a* concentration (0.55–2.51 Log_{10} μg/l Chl *a*).

There are several possible reasons for the poor performance of the Chl *a* transfer function. The first and most obvious possibility is that temperature is a much more powerful driver of chironomid distribution in New Zealand than Chl *a*. This possibility was certainly reflected in the results of the partial CCAs (Table 2). Chl *a* explained only 8.5% of the total chironomid species variation, while temperature (February mean) explained 13.6%. Even though Chl *a* was the only other environmental parameter to remain statistically significant in the partial CCAs (Table 2), the amount of variation that this parameter explained after partialling out the effect of temperature dropped to 4.6%.

The next 3 possibilities assume that New Zealand chironomids may in fact be useful proxies for Chl *a* and certain improvements to the training

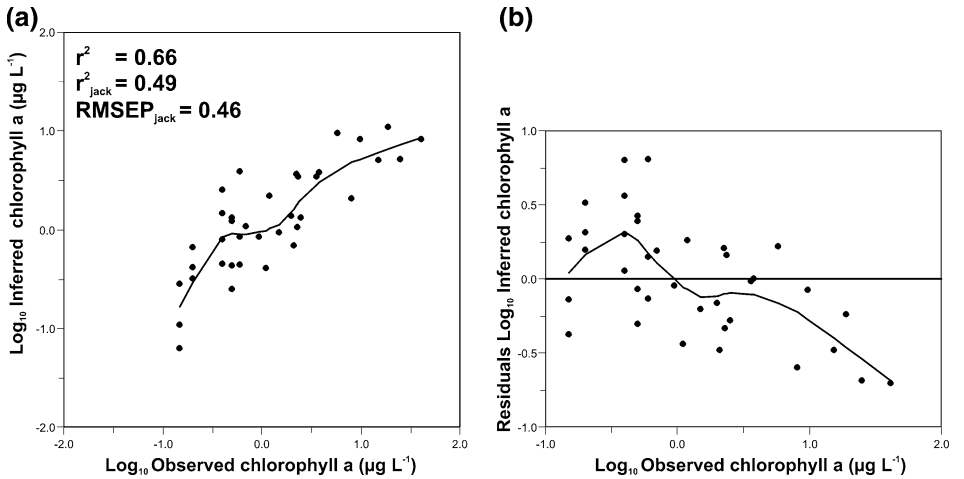

Fig. 7 (**a**) Plot of chironomid inferred Log_{10} inferred Chl *a* vs. Log_{10} observed Chl *a*, and (**b**) observed vs. residual Log_{10} Chl *a* (chironomid-inferred minus observed) using partial least squares (PLS) regression. Loess smoother shown in both figures with a span of 0.45

set may improve the performance of the chironomid-based Chl *a* transfer function. Firstly, improved taxonomy particularly of *Chironomus* (see the earlier discussion regarding this genus) may improve the performance of this model. Secondly, a more extensive set of Chl *a* data will certainly provide a more accurate impression of the long-term conditions in each lake. Brodersen and Lindegaard (1999) used summer mean Chl *a* values in the development of their robust Chl *a* transfer function (which has also been applied by Langdon et al. 2006). Future work should focus on obtaining more Chl *a* measurements to see if this improves the explanatory power of this variable. Long-term Chl *a* records were available for a small number of the lakes in this training set. We decided to use the spot measurements for the sake of consistency because these were available for the majority of the lakes. Finally, increasing the number of lakes at the high end of the Chl *a* gradient may also cause an improvement in the performance of this model.

Conclusions

The analysis of chironomid taxa, and environmental datasets from 46 New Zealand lakes identified temperature (February mean) and lake production (Chl *a*) as the most significant environmental influences on the distribution of chironomid taxa. Temperature explained the highest variation in the chironomid species data and consequently resulted in a more reliable transfer function. The most robust temperature inference model was based on a training set which excluded highly eutrophic lakes. The practice of eliminating other environmental gradients from a training set has been common practice in this field in the past. However, ignoring the effect of nutrients during the exploratory data analyses would have resulted in the failure to identify the problematic distribution of the ubiquitous *Chironomus* morphotype.

Problems attributed to the *Chironomus* morphotype may be resolved by an improved taxonomy of this genus in the future. Until this time the most robust temperature model (with highly productive lakes removed) should be applied with caution. The temperature model will certainly be unreliable if applied to eutrophic lakes or coastal brackish lakes.

Chl *a* was the only other environmental parameter to explain a statistically significant amount of variation in the chironomid taxa. The amount of variation explained by this variable was relatively low and therefore resulted in the production of a transfer function that was not particularly robust. The performance of this model could be improved by an increased taxonomic resolution of the New Zealand chironomid taxa (in particular *Chironomus* and the tribe

Macropelopiini) and by the input of mean Chl *a* concentrations into the model. The spot measurements available for most of the lakes in this study will not be truly representative of typical conditions in each lake.

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Appendix

Table 4 List of Chironomid taxa enumerated in this study

No.	Taxon name	*N*	Hill's *N*2	Maximum	Mean
1	*Ablabesmyia mala* Hutton	15	8.67	9.35	1.14
2	*Camptocladius* De Geer	3	2.40	1.90	0.08
3	*Chironomus* Meigen	46	30.74	100.00	36.71
4	*Cladopelma curtivalva* Kieffer	24	12.33	18.24	2.55
5	*Corynocera* Boothroyd	24	13.26	56.90	9.89
6	*Corynoneura* Winnertz	8	5.31	3.70	0.25
7	*Cricotopus* Boothroyd	12	4.79	6.28	0.34
8	*Cricotopus aucklandensis* Sublette and Wirth	34	12.37	56.07	5.88
9	*Cricotopus hollyfordensis* Boothroyd	1	1.00	0.96	0.02
10	*Cricotopus planus* Boothroyd	1	1.00	0.19	0.00
11	*Cricotopus zealandicus* Freeman	15	9.56	6.18	0.80
12	*Eukiefferiella brundini* Boothroyd and Cranston	4	2.75	3.81	0.16
13	*Eukiefferiella insolida* Boothroyd	1	1.00	2.00	0.04
14	*Eukiefferiella* Thienemann	4	3.28	1.94	0.11
15	*Harrisius pallidus* Freeman	2	1.77	1.90	0.06
16	*Hevelius carinatus* Sublette and Wirth	6	3.12	4.02	0.18
17	*Kaniwhaniwhanus chapmani* Boothroyd	2	1.79	2.27	0.07
18	*Kiefferulus opalensis* Forsyth	1	1.00	11.54	0.25
19	*Larsia* Wiedemann	1	1.00	1.87	0.04
20	Macropelopiini Fittkau	37	19.53	53.85	10.06
21	*Maoridiamesa* Pagast	3	1.34	7.14	0.18
22	*Naonella kimihia* Boothroyd	33	13.24	61.38	8.75
23	*Naonella forsythi* Boothroyd	11	6.57	11.03	1.15
24	*Naonella* ''305'' Unofficial morphotype	3	1.68	2.68	0.08
25	Orthoclad sp. A Boothroyd	5	3.84	1.90	0.13
26	Orthoclad sp. I Unofficial morphotype	5	3.27	2.94	0.13
27	Orthoclad sp. B Boothroyd	2	1.76	1.94	0.06
28	Orthoclad sp. C Boothroyd	11	7.81	3.81	0.40
29	Orthoclad sp. G Unofficial morphotype	6	4.29	1.70	0.12
30	Orthoclad sp. 1/6 Unofficial morphotype	2	1.95	0.89	0.03
31	Orthoclad sp. J Unofficial morphotype	3	2.76	0.85	0.04
32	Orthoclad sp. D Boothroyd	1	1.00	0.50	0.01
33	Orthoclad sp. E Unofficial morphotype	1	1.00	0.64	0.01
34	*Paratrichocladius pluriserialis* Freeman	7	3.61	20.59	1.14
35	*Parachironomus cylindricus* Freeman	2	1.62	1.14	0.03
36	*Paratanytarsus grimmii* Schneider	10	5.05	8.55	0.49
37	*Parochlus* Enderlein	12	4.07	22.11	1.09
38	*Paucispinigera* Stark	9	5.37	4.70	0.30
39	Pentaneurini	3	2.34	2.59	0.11
40	*Pirara matakiri* Boothroyd and Cranston	2	1.52	2.68	0.07

Table 4 continued

No.	Taxon name	*N*	Hill's *N*2	Maximum	Mean
41	*Podochlus* Brundin	1	1.00	0.50	0.01
42	*Podonomus* Philippi	2	1.91	2.01	0.07
43	*Polypedilum* Boothroyd	25	7.07	80.95	5.74
44	*Pseudochironomus* Malloch	2	1.81	0.46	0.02
45	*Smittia verna* Hutton	6	4.42	3.74	0.24
46	*Stictocladius* Edwards	1	1.00	1.87	0.04
47	*Tanytarsus* Boothroyd	14	8.58	3.41	0.38
48	*Tanytarsus funebris* Freeman	30	14.30	35.78	5.34
49	*Tanytarsus vespertinus* Hutton	24	9.91	32.14	4.22
50	*Xenochironomus canterburyensis* Freeman	3	2.99	0.96	0.06

Numbers correspond to CCA results (Fig. 3). The author of each taxonomic name is shown. The number of lakes were each taxon occurred (*N*), effective number of occurrences (Hill's *N*2), maximum and mean relative abundances (as a percent) are shown

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Chironomid-based reconstructions of summer air temperature from lake deposits in Lyndon Stream, New Zealand spanning the MIS 3/2 transition

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Abstract

We present chironomid-based temperature reconstructions from lake sediments deposited between ca 26,600 cal yr BP and 24,500 cal yr BP from Lyndon Stream, South Island, New Zealand. Summer (February mean) temperatures averaged 1 °C cooler, with a maximum inferred cooling of 3.7 °C. These estimates corroborate macrofossil and beetle-based temperature inferences from the same site and suggest climate amelioration (an interstadial) at this time. Other records from the New Zealand region also show a large degree of variability during the late Otiran glacial sequence (34,000–18,000 cal yr BP) including a phase of warming at the MIS 2/3 transition and a maximum cooling that did not occur until the global LGM (ca 20,000 cal yr BP).

The very moderate cooling identified here at the MIS 2/3 transition confirms and enhances the long-standing discrepancy in New Zealand records between pollen and other proxies. Low abundances (<20%) of canopy tree pollen in records from late MIS 3 to the end of MIS 2 cannot be explained by the minor (<5 °C) cooling inferred from this and other studies unless other environmental parameters are considered. Further work is required to address this critical issue.
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1. Introduction

The ability to accurately reconstruct past climates is a reflection of our capability to predict major climate change in the future. Since the initiation of Climate Long-range Investigation, Mapping, And Prediction (CLIMAP) almost 30 years ago (CLIMAP project members, 1976) the Last Glacial Maximum (LGM) (23,000–19,000 cal yr BP (Mix et al., 2001) has remained an important benchmark for the testing of global climate models. The LGM represents the most recent, well recorded, example of major natural climate change that lies within the limits of a large number of dating techniques. Therefore it is possible to obtain a large amount of paleoclimatological data which not only serves to validate climate models but direct their construction.

Recent studies (Crowley and Baum, 1997; Crowley, 2000; Kohfeld and Harrison, 2000; Moreno et al., 2005) have emphasised the importance of an 'earth-system' approach to model development; climate models should account for possible effects of ocean–atmosphere–cryosphere–biosphere interactions. Global climate models have, until recently been based largely on reconstructions of sea surface temperatures (SSTs) (e.g. CLIMAP, 1981) because SST reconstructions are based on a globally extensive dataset of modern analogues (e.g. Barrows and Juggins, 2005). However, observations based on an ever increasing terrestrial dataset (e.g. dust records, lake-levels, faunal and floral-based reconstructions, and paleo snow-line elevations) have revealed inconsistencies between terrestrial conditions inferred from SST-based global climate models and inferences based on local proxy data (Pinot et al., 1999).

Terrestrial paleoclimate data from the Northern Hemisphere far exceeds the quantity of data from the southern latitudes. The few quantitative estimates for land-based LGM temperature anomalies in the Southern Hemisphere

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have been based on snow-line depressions (Hilton et al., 1994; Bacon et al., 2001), TEX_{86} lake surface temperatures (LSL) (Powers et al., 2005), and pollen-based estimates (e.g. Bush et al., 2004). Increasing this dataset is essential for the purposes of global climate model development and validation.

Despite being identified as a key site for future investigation into LGM climate variability (Broecker, 1997), quantitative paleoclimate data generated for the LGM period in New Zealand is also limited. These data are especially important, as recent studies (Suggate and Almond, 2005; Vandergoes et al., 2005) indicate that so-called 'LGM' cooling in New Zealand may have begun as early as 34,000 cal yr BP; predating the real LGM by 11,000 years. The last glacial cycle (ca 74,000–ca 11,500 cal yr BP) is locally known as the Otira Glaciation (Suggate, 1990). In this paper, we refer to the period between 34,000 and 18,000 cal yr BP in New Zealand which corresponds to a series of major ice advances (Suggate and Almond, 2005) as the late Otiran glacial sequence (LOGS).

We avoid the use of the term LGM as the term 'LGM' as it is officially defined denotes the last period of maximum global ice volume (Mix et al., 2001). The use of this term to label local ice advances (even though there are Southern Hemisphere correlatives (Denton et al., 1999b)) has already caused confusion. We use the term 'sequence' because there were several major ice volume fluctuations in New Zealand during this time (Suggate and Almond, 2005) and a great deal of climate variability (Sandiford et al., 2001, 2003; Hägg and Augustinus, 2003; Hormes et al., 2003; Vandergoes et al., 2005). Although some large ice advances occurred early in the LOGS (Suggate and Almond, 2005) it appears that the greatest amount of cooling did not occur until the time of the global LGM (Barrows and Juggins, 2005).

Pollen-based estimates imply mean annual temperature (MAT) depressions for the LOGS ranging from 4 to 7 °C (Soons, 1979; McGlone et al., 1993; Shulmeister et al., 2001). Beetle-based mutual climate range (MCR) reconstructions from middle (ca 27,000–22,000 cal yr BP) of the LOGS suggest a maximum cooling of between 1.9 and 5 °C in summer (February mean) and 2.2 and 6 °C for winter (July mean daily minimum) (Marra et al., 2004, 2006).

Previous studies elsewhere in the world (Seppa et al., 2004) have used pollen-based transfer functions to infer past climate conditions. Despite the fact that pollen has been the most widely used proxy for climate change in New Zealand, only one study (Norton et al., 1986) has explored the possibility for the development of pollen-based transfer functions. The resulting transfer functions were not robust enough to be confidently applied to the fossil pollen record. Therefore generalisations about climate have continued to be inferred from the modern species distribution of taxa found in the fossil record. A major climate deterioration spanning the entire LOGS has been inferred from the low abundance of pollen belonging to canopy trees (Podocarpaceae and *Nothofagus*) and the abundance of herb and grass pollen in records spanning approximately 34,000–18,000 years ago (Moar, 1980; Moar and Suggate, 1996; Vandergoes et al., 2005, Fig. 4).

Very little cooling has been inferred from some of the beetle-based reconstructions (Marra et al., 2004, 2006) and from recent climate model-based air temperature inferences (Weaver et al., 1998; Bush and Philander, 1999). A slight increase in canopy tree pollen abundance is recorded in some LOGS pollen records at the MIS 3/2 transition (Vandergoes et al., 2005). However, if the inferences of mild cooling from other proxies are correct, most of the North Island and the northern half of the South Island below 600–700 m above sea level (asl) should have been forested (McGlone et al., 1993). Therefore a number of other environmental factors including altered CO_2 regimes, fire, drought, invasion of cold maritime polar air masses, and strong winds have been cited as possible causes for the lack of forest cover during the LOGS (McGlone and Bathgate, 1983; McGlone, 1985, 1988).

Given the problems with pollen-based reconstructions and the paucity of other quantitative proxies for climate in New Zealand, there is an obvious need to develop new proxies. This paper presents results of the first chironomid-based summer temperature reconstructions from lake deposits in New Zealand. The site reported comes from the banks of Lyndon Stream in the high country of Canterbury, on the eastern side of South Island of New Zealand (Fig. 1) and lies in the middle (~26,500–24,500 cal yr BP) of the LOGS. Studies elsewhere in the world have validated the ability for chironomid-based transfer functions to predict air temperatures (Walker et al., 1991; Olander et al., 1997). The locality was chosen because there are existing qualitative temperature estimates based on macrofossils (Soons and Burrows, 1978) and quantitative temperature estimates from beetles (Marra et al., 2006) for this site. Here, we provide temperature estimates for the complete section of lake silts preserved at this site. The results from this study serve not only to provide a more complete picture of climate conditions in New Zealand during the LOGS at this locality, but also enable comparison of the chironomid-based temperature estimates with independent proxies.

2. Site description

2.1. Physiography and site context

Lyndon Stream is located in the Acheron Valley, in the eastern foothills of the Southern Alps, South Island, New Zealand (Fig. 1). The study site is at an altitude of 700 m asl. Locally, the eastern foothills reach elevations of up to 2300 m and are composed largely of moderately indurated Triassic–Jurassic metasediments belonging to the Torlesse Supergroup (Bradshaw, 1972). The local geomorphology has been profoundly influenced by a series of Late Pleistocene glacial advances (Soons, 1963; Suggate, 1990).

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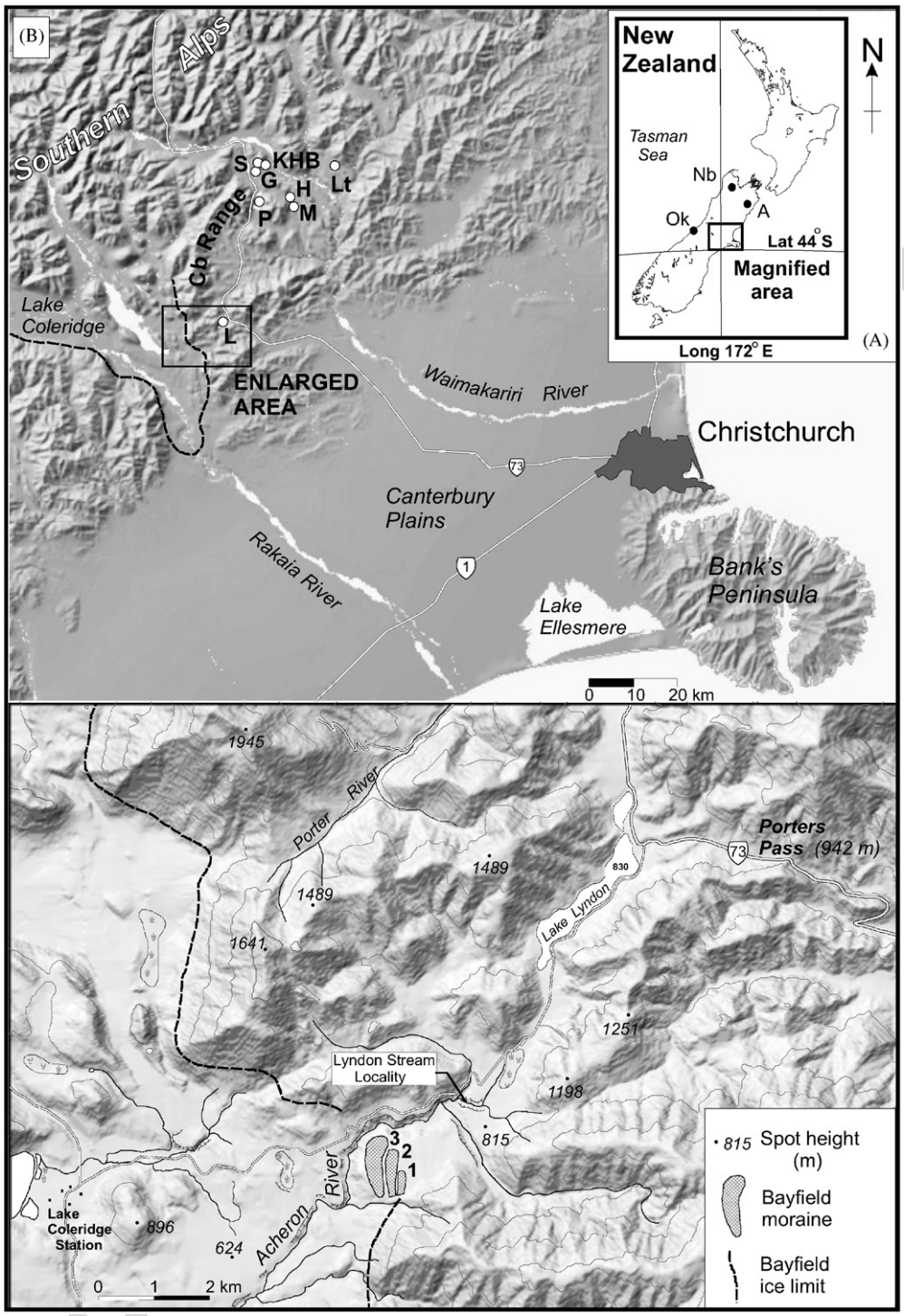

Fig. 1. The location of the study site and other features mentioned in the text. (A) Ok= Okaritio Bog, Nb= Nettlebed Cave, A= Awatere Valley. (B) Cb Range= Cragieburn Range, KHB= Kettlehole Bog. Lakes proximal to the study site: S= Lake Sarah, G= Lake Grasmere, Lt= Lake Letitia, H= Lake Hawdon, M= Lake Marymere, P= Lake Pearson, L= Lake Lyndon.

Of particular relevance to this study, are the multiple ice advances from west to east along the upper reaches of the Rakaia River (Fig. 1) (Soons, 1963). Moraines and outwash terraces in the Rakaia valley provide evidence for five main glacial sequences, locally named the Acheron, Bayfield (inferred to be late Otiran in age), Tui Creek, Woodlands and Hororata advances (in order of increasing age) (Soons and Gullentops, 1973).

The Acheron Valley is a splay valley of the Rakaia and the valley is partly occupied by moraines and outwash fans of the Rakaia Valley glaciers. A series of three moraine ridges lies at the southern end of the Acheron

Valley (Fig. 1). Soons and Burrows (1978) argued that these moraines represented glacial limits during the Bayfield ice advance in the Rakaia Valley. Two early advances (Bayfield 1 and 2) are represented by the two highest moraine ridges, while the Bayfield 3 advance is represented by the lowest of the three moraines (Fig. 1). The Lyndon Stream sediments have been deposited in an incision in the Bayfield 2 outwash surface. Therefore the deposition of the Lyndon stream sediments post-dates Bayfield advances 1 and 2 and pre-dates the Bayfield 3 advance. Radiocarbon ages from the deposit (Soons and Burrows, 1978) confirm a middle LOGS age for these deposits and are in fact the only published age control on the Bayfield advances.

2.2. Climate

The local climate is a product of the interaction of the Southern Hemisphere westerlies with the rugged topography of the Southern Alps (Fig. 1) (Sturman and Wanner, 2001). Orographic uplift of the airflow off the Tasman Sea (Fig. 1) results in an extreme contrast in average rainfall between the western and eastern sides of the mountains. Average annual precipitation near the divide on the western side of the Southern Alps can reach well over 10,000 mm, while the eastern coastal plains and mountain basins receive an average annual rainfall of 600 mm (Griffiths and McSaveney, 1983).

The mean annual total rainfall at the Lake Coleridge climate station (364 m AMSL) about 8 km west of the site (Fig. 1) is 833 mm (NIWA, unpublished data). The mean annual temperature at the same station is 10.4 °C. The late summer (February) mean (14 °C) and winter (July) mean minimum (−1 °C) for the study site was extracted from a climate surface fitted to data from 346 weather stations covering a period of 30 years (Leathwick et al., 1998). Salmon (1992) reported temperature data for the tree-line (1341 m asl) from the nearby Cragieburn Range (Fig. 1). The February mean for this altitude was 10 °C, while the July mean minimum was −3.5 °C.

2.3. Vegetation

Pollen records (Burrows and Russell, 1990) and macrofossils (Burrows, 1995) provide evidence for the existence of a mixed podocarp/angiosperm (e.g. *Prumnopitys taxifolia*) forest in the lowlands and a *Nothofagus* (*Nothofagus solandri* var *cliffortoides*) forest on the higher slopes (up to 1400 m) from at least 3000 years ago. Only patches of this original forest cover remain, after being largely destroyed by fire in the last 800 years after the arrival of Polynesians (ca 1300 AD) and Europeans (ca 1840) (Burrows and Russel, 1990; McGlone and Wilmshurst, 1999). Short-tussock grassland (*Festuca novae-zelandiae* and *Poa colensoi*) and patches of scrub (*Leptospermum scoparium*, *Discaria toumatou*, *Ozothamnus leptophyllus*, *Coprosma propinqua*, *Hebe* spp., and *Dracophyllum* spp.) form the dominant vegetation cover at present.

2.4. Stratigraphy and lithology

The Lyndon Stream has incised a ~14 m deep gully into the sediments on the eastern side of the Acheron Valley, exposing a sequence of glacial till, lake silts, sand, silt, and alluvium. Soons and Burrows (1978) described the sedimentology for the entire section, and derived radiocarbon dates from organic material in the basal lake silts and upper *Sphagnum* silts. Macrofossils and pollen were also extracted from a sample from the base of the lake silts and described. The following description is a summary of Soons and Burrows (1978).

Basal 2 m: Brownish grey till; upper 20–30 cm iron-stained.

⩽6 m: Fine blue-grey laminated silts, with plant remains consisting chiefly of *Myriophyllum elatinoides*. A conventional radiocarbon age of 22200 +/−750 ^{14}C yr BP (NZ 3940) was obtained from a sample collected at the base of the silts where they overly the till.

2 m: Brown laminated silts with occasional fine gravel layers.

2.5 m: Brown sands and silts with occasional fine gravel bands. *Sphagnum* silts occur at the top of this deposit. A conventional radiocarbon age was derived from the *Sphagnum* silts was 19,200 ^{14}C ± 550 yr BP (NZ 4298).

Top 1.5 m: Locally derived subangular brown greywacke, horizontally bedded and alternating with brown sandy layers.

2.5. Detailed description of the lake silts

The majority of this paper deals with the chironomid stratigraphy of the lake silts, therefore a more detailed description of this horizon is provided in the following section.

The lake silts were carefully examined while samples were collected for this study. Soons and Burrows (1978) described a 6 m thick laminated lake silt horizon. We could not find an exposure in the Lyndon Stream cutting were the basal lake silts were 6 m thick. The section sampled for this study was only ~3.5 m thick. A close inspection of the lake silts also revealed that individual layers that were <1 cm thick were quite rare. Therefore it would be more accurate to describe the lake sediments as bedded (Schnurrenberger et al., 2003). True laminae are more common near the transition between the bedded lake silts and the overlying silts.

Individual beds ranged in thickness from 1–10 cm and comprise alternating bands of light and dark-coloured material. Bedding was particularly weak in places where bedding contacts were indistinct (change noted over >1 cm) and individual beds were discontinuous. Undulating contacts between beds were also common.

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3. Methods

3.1. Sediment sampling and processing

The entire section, from the base of the bedded lake silts to the top of the upper sandy-silt unit, was sampled at approximately 25 cm intervals for chironomid analysis. Two cm thick slabs of sediment (~30 cm^3) were removed from the outcrop face using a large sharp knife. Large sections of the upper sandy-silt unit appeared to be unsuitable for the preservation of chironomid remains (coarse grain size, evidence of low organic content, cross-bedding, etc.). Therefore, samples were only taken from the fine-grained silty-clay units that were present in this part of the section. A preliminary examination revealed that chironomids were absent even from these horizons in the upper sandy-silt unit.

Sediment samples were processed for chironomids following a modified version of the method outlined in Walker (2001). Samples were weighed, deflocculated in hot 10% KOH and washed through a 93 μm mesh with copious amounts of distilled water. Samples were then transferred to a Bogorov counting tray and examined for invertebrate remains under a dissection microscope at 50 × magnification. Heiri and Lotter (2001) and Quinlan and Smol (2001) have shown that a sample size of 45–50 head capsules provides an adequate representation of chironomid diversity in a sample. Sufficient sediment (typically 10 mL) was processed in order to obtain this minimum head capsule abundance.

Chironomid head-capsules were mounted on glass slides in a drop of lactophenol PVA and covered with a glass coverslip. Head-capsules were mounted ventral side up to facilitate identification. Chironomids were identified using a transmission light microscope with the aid of publications by Schakau (1993), Boubee (1983), Forsyth (1971), Winterbourne et al. (2000), and identification guides by Boothroyd (1994, 2002, 2004). The division of the genus *Chironomus* was based on unpublished morphological and karyotypic data from Jon Martin and Don Forsyth.

A small sample from each horizon was weighed then dried in an oven at 100 °C for 24 h to allow the calculation of head capsule concentrations per gram of dry sediment. Oven dried samples were then heated to 550 °C for 12 h to allow the calculation of the organic content (loss-on-ignition) for each sample.

3.2. Data analysis and presentation of results

The abundance of each chironomid taxon was expressed as a percentage of the total head-capsule count for each individual horizon. Simuliidae ('black flies', *Austrosimulium*) head-capsules were also found, these were expressed as a percentage of the total head-capsule count (chironomids and Simuliidae combined). Taxon abundances were displayed relative to stratigraphic depth using the computer programme C2 (Juggins, 2003). Zonation of the chironomid stratigraphy was achieved using the CONISS (constrained incremental sum of squares) function in Zone 1.2 (Juggins, 1992). The analysis was based on the chironomid percentage data standardized to a mean of zero and to unit standard deviation (Grimm, 1987). The Shannon Weaver Index (H') was used as a measure of chironomid diversity. $H' = -\Sigma Pi \ln Pi$, where Pi represents the proportion of the ith taxon in the sample (Begon et al., 1986).

Exploratory analysis of the fossil chironomid assemblages from the Lyndon Stream site were investigated using CANOCO version 4.5 (ter Braak and Šmilauer, 2002). Fossil samples were plotted as passive samples in a canonical correspondence analysis (CCA) ordination plot of modern chironomid samples and environmental variables from a 46-lake New Zealand training set (Woodward and Shulmeister, in press). This training set was developed for the construction of transfer-functions for temperature (February mean) and lake production (chlorophyll *a*). The five most productive lakes (chlorophyll $a \geqslant 9$ μg/L) were removed from the final temperature model (Woodward and Shulmeister, in press). Only lakes that were included in the final temperature transfer-function ($n = 35$, the 'temperature training set') were used in the ordination.

The division of the *Chironomus* genus was not performed during the construction of the original training set. We therefore re-counted the slides to check the identification of this genus. Species were only included in the analysis if they were present at an abundance of $\geqslant 2\%$ in at least 2 lakes in the modern training set. Removing rare species was found to improve the statistical significance of the relationship between temperature and chironomid assemblage composition (Woodward and Shulmeister, in press).

Fossil samples were joined as a 'time-track' to allow the interpretation of changes in fossil chironomid assemblage composition with respect to environmental parameters with a significant ($p \leqslant 0.05$) influence on the distribution and abundance of chironomid taxa in the temperature training set. Partial CCAs were used to determine which environmental variables explained the greatest amount of variation in the species data in the temperature training set. The statistical significance of each environmental variable was tested by a Monte Carlo permutation test (999 unrestricted permutations under the full model).

Several lakes in the vicinity of the sample locality (Lyndon, Grassmere, Letitia, Sarah, Hawdon, and Marymere (Fig. 1)) were not included in this training set. Chironomid species data from these sites was obtained from Schakau (1993). Schakau did not measure all the significant environmental variables during sampling visits. For the sake of comparison, these lakes were fitted passively into the CCA plot, based only on their species composition. One proximal lake (Lake Pearson) was included in the 35-lake temperature training set, so was plotted in the CCA based on both species and environment data.

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February mean air temperatures were reconstructed using a weighted averaging-partial least squares (WA-PLS) model (2 components) with an r^2_{boot} of 0.75 and a root mean-squared error of prediction (RMSEP) of 1.55 °C. February mean temperature values were untransformed while species percentage data was square root transformed (Woodward and Shulmeister, in press).

4. Results

4.1. Chironomid stratigraphy and taxonomic notes

The results from the chironomid analysis are shown in a percentage diagram in Fig. 2. Fifteen chironomid taxa were recovered from the Lyndon Stream section. The most common taxon in the Lyndon Stream section belonged to the genus *Chironomus*. The other 13 taxa were present in low abundances (<10%) for the entire section except for *Corynocera* and *Naonella forsythi*, which exceeded 10% relative abundance in Zone 2 and Zone 4, respectively.

Until recently it was impossible to distinguish the three previously described *Chironomus* species from the New Zealand mainland (Hudson, 1892; Kieffer, 1921; Freeman, 1959) based on head-capsule morphology alone. Jon Martin and Don Forsyth (unpublished) have performed extensive morphological and karyotypic studies of New Zealand *Chironomus* larvae and now conclude that nine species of *Chironomus* exist on the New Zealand mainland. However, it is only possible to reliably distinguish one of those nine species from the other eight based on head-capsule morphology alone.

Jon Martin and Don Forsyth (unpublished) identified *Chironomus* sp. a based on the larval karyotype and observed that this species always had a large number (>60) striations on the ventromental plate. It is almost certain that this species is actually the *Chironomus zealandicus* that was originally described by Hudson (1892) (Jon Martin, pers. commun.). Until this link is confirmed beyond doubt we will refer to this species as *Chironomus* sp. a. The other eight species identified by Jon Martin and Don Forsyth always had a smaller (<60) number of striations on the ventromental plate. All the head-capsules belonging to *Chironomus* from this record had less than 60 striations on the ventromental plate. We refer to this morphological type as *Chironomus* spp. as it is not possible to reliably distinguish between the eight karyotypes identified by Jon Martin and Don Forsyth (unpublished) based on head-capsule morphology alone.

All of the *Chironomus* head-capsules in the temperature training set used in this study also belonged to the *Chironomus* spp. type. *Chironomus* sp. a was only present in abundances ⩾2% in the five highly productive (chlorophyll $a \geqslant 9\,\mu g/L$) lakes that were removed from the temperature training set. *Chironomus* spp. was present in abundances ⩽2% in two other lakes; a lowland mesotrophic lake and a high altitiude microtrophic lake (trophic definitions after Burns et al., 2000). Therefore the division of the *Chironomus* genus into two morphological types did not affect the performance of the temperature transfer function.

The chironomid record was divided into four zones based on the total dispersion values produced by the CONISS cluster analysis in Zone 1.2. 2 taxa (*Chironomus* spp. and *Naonella kimihia*) dominated the chironomid assemblages for the entire section. The main distinctions between the four chironomid zones are the presence of Macropelopini and *Corynocera* in Zone 2, the gradual decline in abundance of *Naonella kimihia* from Zone 1–4 and the appearance of a number of orthoclad taxa in Zone 4.

The average diversity for the entire record was low ($H' = 0.4$), with two peaks of slightly higher diversity in Zone 2 and 4. Head-capsule concentrations were highest in Zone 1 (~50–80 head capsules per gram dry sediment (HC/g^{-1})) and dropped abruptly to remain low (<10 HC/g^{-1}) for the rest of the record. Higher head-capsule concentrations also coincided with the tendency for a slightly higher organic content (⩾5% LOI) in the basal metre of the record.

Black fly (Simuliidae) head-capsules (*Austrosimulium*) were also present in low percentages in Zone 3 and 4. *Austrosimulium* counts were not included in the zone analysis. Percentage abundance of *Austrosimulium* was calculated as a fraction of all head-capsules (chironomids and Simuliidae). *Daphnia* (Cladocera) ephippia (resting eggs) were also common between 200 and 220 cm (the Zone 1/2 transition).

4.2. Ordination

A 'time-track' CCA plot of the Lyndon Stream Fossil samples with respect to modern samples and significant environmental variables is shown in Fig. 3. Five variables emerged as significant ($P<0.05$) drivers of chironomid distribution and abundance: February mean temperature, chlorophyll *a*, total nitrogen, conductivity and reactive phosphorus. February mean temperature was responsible for the greatest proportion of the total variation in the chironomid species data (15%), followed by chlorophyll *a* (9.2%) and reactive phosphorus (7.2%).

February mean temperature showed the highest degree of correlation with CCA axis 1 (−0.82), while conductivity and reactive phosphorus were most closely correlated with CCA axis 2 (~0.40). Major shifts in the composition of the fossil assemblages in the Lyndon Stream section correspond to CCA axis 2 (conductivity and reactive phosphorus) rather than CCA axis 1 (the temperature gradient). Most of the fossil assemblages plot closely in ordination space to assemblages from modern sediment samples taken from lakes proximal to Lyndon Stream.

4.3. Quantitative temperature reconstructions

Reconstructed late summer average (February mean) temperature values for the entire record plotted between

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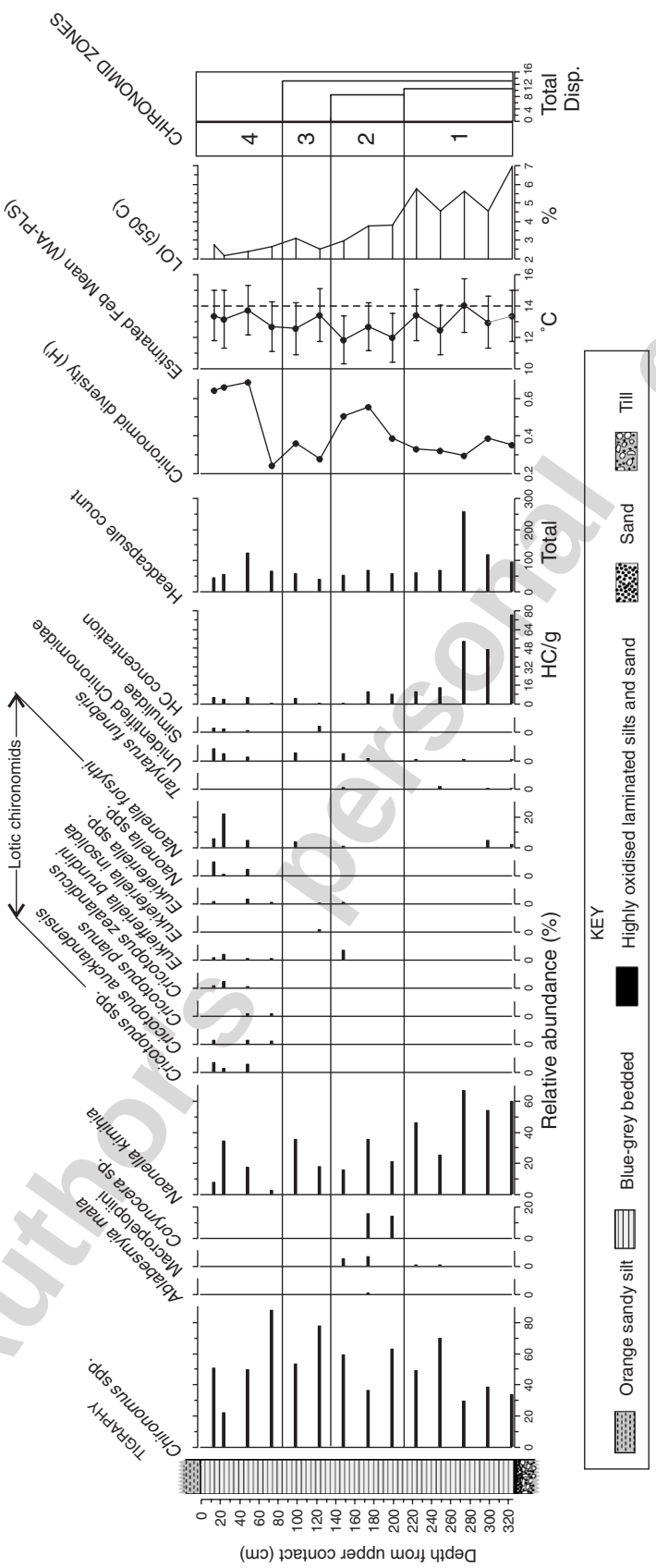

Fig. 2. Chironomid percentage diagram and temperature reconstruction from the Lyndon Stream section. Dashed vertical line in the temperature reconstruction represents the modern February mean for the sample site.

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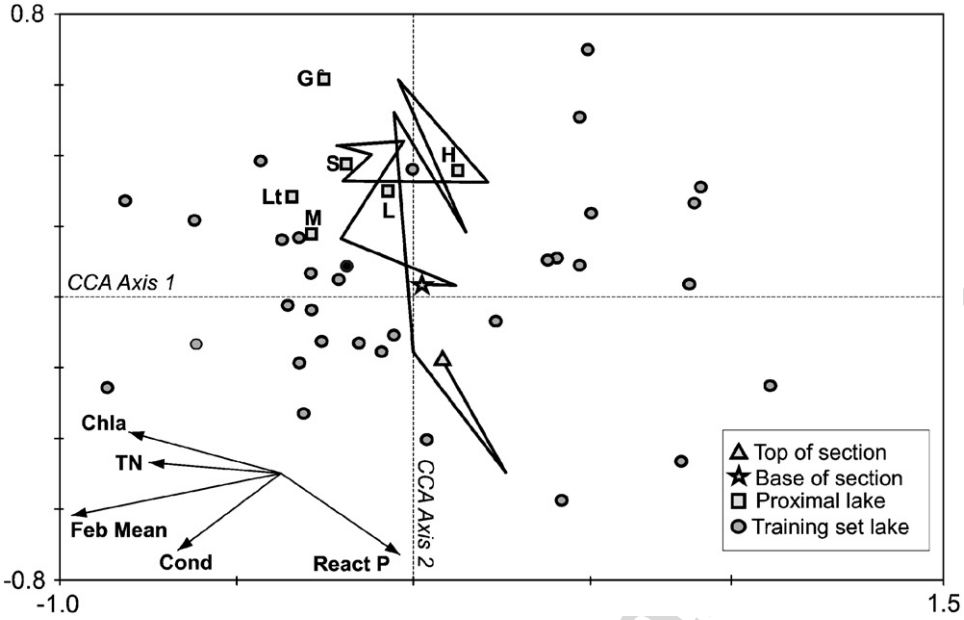

Fig. 3. CCA "time track" plot of chironomid samples from the Lyndon Stream Lake silts. The proximal lakes (abbreviations as in Fig. 1) and the fossil samples have been fitted passively in the ordination. The fossil samples have been connected in order of stratigraphic position by a solid black line. The positions of the training set lakes are shown relative to the main significant ($p<0.05$) environmental gradients. Feb Mean= February mean, Cond= conductivity, TN= total nitrogen, Chl*a*= chlorophyll *a*, React P= reactive phosphorus.

10.3 and 15.7 °C, within the margins of error (Fig. 2). This is equivalent to a maximum cooling of 3.7 °C and a warming of 1.7 °C relative to the modern February mean (14 °C, shown as a dashed line in Fig. 2). There is a general trend of cooling from the base of the section to mid section, with temperatures increasing again towards the top of the record. However, all temperature reconstructions overlap when the sample specific error is taken into account. The maximum inferred cooling (3.7 °C) coincides with chironomid Zone 2. The average cooling inferred for the entire record is equivalent to ~1 °C relative to the modern February mean.

5. Discussion

5.1. Ecological interpretation

The evidence from chironomids (this study) and macrophyte remains (Soons and Burrows, 1978) suggest that paleolake Lyndon was a shallow (<6 m water depth) oligotrophic to mesotrophic lake. The remains of *Myriophyllum elatinoides* and *Potamogeton cheesmanii* were particularly abundant in the basal sample described by Soons and Burrows (1978). Although these species are restricted to water depths of <6 m (Clayton et al., 1989), it could also be possible that these sediments were deposited in deeper water if the macrophyte remains were transported from the lake margin. However, the remains of macrophytes that are typical of deeper water (e.g. Charophyceae (Clayton et al., 1989)) were absent from these sediments.

Fossil chironomid species assemblages closely resemble lakes in the modern training set that range from microtrophic to oligotrophic (chlorophyll $a = 0.33 - 3\,\mu g/L$). It is possible that mesotrophic conditions occurred at some stage in paleolake Lyndon, as the taxa present in this record have reasonably high tolerances for trophic level ranging from microtrophic to mesotrophic (chlorophyll $a = 0.33 - 5\,\mu g/L$). It is highly unlikely that eutrophic (chlorophyll $a > 5\,\mu g/L$) conditions occurred at any time because *Naonella kimihia* is rare in such lakes (Woodward and Shulmeister, in press). *Chironomus* sp. a was also absent from this record. A re-examination of the original slides for the 46 lake training set (Woodward and Shulmeister, in press) revealed that *Chironomus* sp. a was the dominant taxon in eutrophic lakes.

The main changes in fossil chironomid assemblages are parallel to CCA axis 2 (Fig. 3). This suggests that major changes in conductivity and reactive phosphorus had a significant control on the ecology of this lake. There is a general trend towards lower conductivity from about 120–320 cm in the record (the first 9 samples from the base). Both Macropelopini and *Corynocera* are relatively common in Zone 2. Both of these taxa were typical of micro- to mesotrophic lakes with low conductivity in the modern training set (Woodward and Shulmeister, in press). Engstrom et al. (2000) cite evidence for a progressive loss of pH, alkalinity and base cations from lakes situated in recently deglaciated terrain. Engstrom et al. argue that this is due to the effects of vegetation succession, soil development and hydrologic change.

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Even though the sample specific errors for the temperature reconstruction overlap (Fig. 2), it is also possible that the change in chironomid fauna from Zone 1 to 2 represents a slight cooling. Ephippia (resting eggs) belonging to *Daphnia* (Cladocera) were common in the sediments in the lead up to this switch. Cladocera are known to produce ephippia to survive phases of unstable conditions and environmental stress (e.g. lake desiccation or lake freezing) (Deng, 1996; Sarmaja-Korjonen, 2003). The cooling inferred from the chironomid-based temperature transfer function suggests the latter.

There is a subsequent major increase in conductivity and reactive phosphorous at the top of the section. The reason for the rapid increase in conductivity and reactive phosphorus at the top of the section is not clear. This could be related to a gradual infilling of the lake or an increase in the input of dissolved solids into this water body.

Soons and Burrows (1978) suggest the possibility that the basal lake silts comprised glacially derived sediments, and that the change from lake silts to the coarser orange sandy silts further up-section represents the migration of an alluvial fan into the lake. The migration of an alluvial fan into the lake is supported by the increase in chironomid (and other taxa) that are typical of running water (= lotic habitats) in Zone 4 (Fig. 2). *Cricotopus*, *Eukiefferiella*, and *Naonella* are common components of New Zealand river macroinvertebrate communities (Milner et al., 2001). The presence of head-capsules from the blackfly *Austrosimulium* (Simulidae), another common taxon in streams and rivers (Collier et al., 1998), also suggests the proximity of this site to a stream or river. There is no chironomid-based evidence for the proximity of ice during the deposition of the lake silts. The absence of the chironomid taxon *Maoridiamesa* in the lotic assemblage (and elsewhere in the record) implies that even though there was possibly a slight cooling mid-section, this site was not close to a glacier face during the deposition of the lake silts (Milner et al., 2001).

5.2. Implications for New Zealand LOGS climate conditions

There are two published radiocarbon ages that constrain the chronology of the lake silts. A basal age of 22,200 +/−750 ^{14}C yr BP (NZ 3940), and an age from the upper *Sphagnum* silts of 19,200 ^{14}C ± 550 yr BP (NZ 4298) (Soons and Burrows, 1978). These radiocarbon ages were calibrated using INTCAL98 (Stuiver et al., 1998) and yielded ages of 26,651 ± 1009 cal yr BP for the base of the silts, and 23,026 ± 646 cal yr BP for the upper *Sphagnum* silts. The chironomid record only extends to the top of the lake silts, but there is no radiocarbon age for the top of this unit at present. Therefore an approximate age for the top of the lake silts of 24,500 cal yr BP was estimated by interpolation. The uncertainty of the basal radiocarbon age (27660–25642 cal yr BP) suggests the possible existence of the Kawakawa tephra (26,500 cal yr BP) at the base of the lake silts; this was not seen in the field. We are aware of one luminescence age and one AMS radiocarbon age (unpublished) that may reduce the age range of the base of the lake silts by up to 800 yr. Further dating of this deposit and confirmation of the presence/absence of the Kawakawa tephra will serve to further constrain the chronology of these deposits, but a mid-LOGS (MIS 3/2 transition) age seems secure.

The chironomid-based temperature reconstructions are in agreement with the beetle-based estimates of Marra et al. (2006) and the macrofossil-based inferences of Soons and Burrows (1978). Therefore the chironomid-based temperature model seems to be producing reasonable reconstructions. Marra et al. (2006) inferred a February mean that ranged from 0.5 °C warmer to 1.9 °C cooler than the modern February mean from a sample taken at the base of the Lyndon Stream section (Fig. 4). Soons and Burrows (1978) noted the presence of seeds and pollen from *Potamogeton cheesmanii*, *Montia fontanam* and *Myriophyllum elatinoides* in a stratigraphically equivalent sample. These plants are present up to an altitude 400 m higher than the Lyndon Stream locality today. An increase in altitude of this magnitude would be equivalent to a reduction in the February mean of up to 2.5 °C.

The chironomid-based reconstruction from the same horizon (300 cm depth from the top of the lake silts) inferred a February mean between 0.5 °C warmer and 2.5 °C cooler than the modern February mean. Therefore, the chironomid estimate falls within the range of temperature reconstructions based on the beetles and macrofossils. Based on all the samples, the chironomid-based reconstruction estimates temperature variations between 1 °C warmer and 3.7 °C cooler than the modern February mean.

We believe that it is highly unlikely that temperatures would have been warmer than the modern February mean at this time. Several warm stenothermic species that are present in lakes proximal to Lyndon Stream (Fig. 1) are absent from the Lyndon Stream lake sediments. *Cladoplema curtivalva* and *Polypedilum* occur in modern oligotrophic to mesotrophic lakes proximal to this study site. The temperature optima and tolerances for these species were calculated by weighted averaging of species and environmental data from the modern training set (Woodward and Shulmeister, in press) in the software package C2 (Juggins, 2003). The distribution and abundance of *Cladoplema curtivalva* showed a significant ($P = 0.001$) correlation to February mean temperature, while the distribution of *Polypedilum* was not significantly related to temperature ($P = 0.06$). The lower limit for the survival of *Cladoplema curtivalva* was estimated to be 12.9 °C (including the error limits for the tolerance and the optima). We conclude that if February mean temperatures were above this threshold, *Cladoplema curtivalva* should be present in the Lyndon Stream record. We therefore suggest a temperature depression of between 1.1 and 3.7 °C. This inferred upper limit for the temperature reconstruction also agrees with the conservative beetle-based estimate

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(Marra et al., 2006) i.e. the estimate based on the known temperature range of the modern species.

When calculating the actual decrease in February mean temperature for this period it is necessary to take into account the ca 120 m sea-level drop that began ~30,000 cal yr BP and extended to ~19,000 cal yr BP (Lambeck et al., 2002). This drop in sea-level would be equivalent to a drop in temperature of ca 0.72 °C based on a lapse rate of 0.6±0.1 °C/100 m (Hales and Roering, 2005). This means that the beetles (Marra et al., 2006) and the macrofossils (Soons and Burrows, 1978) are actually estimating a temperature variation between ~1.2 °C warmer and ~1.8 °C cooler than the sea-level adjusted February mean from the single basal sample. Based on all the samples, the chironomid-based reconstruction estimates temperature variations between ca 0.4 and 3 °C cooler relative to the sea-level-adjusted February mean.

Soons and Burrows (1978) concluded that the Lyndon Stream lake sediments were deposited during an interstadial, based on the macrofossils and the relationship between the lake sediments and the outwash surfaces associated with the Bayfield moraines (Fig. 1). The temperature reconstructions from this study and that of Marra et al. (2006) corroborate the interpretation of Soons and Burrows (1978). The absence of a typical ice-proximal chironomid assemblage throughout the section also precludes the presence of glacial ice in the valley at this time. The lake represents an ice-free period in this valley between advances and indicates that conditions warmed up to full or near-full interglacial values. This record confirms the existence of an interstadial in the previously monotonically cold period (~34,000–18,000 cal yr BP) in New Zealand.

The existence of a significant amount of climate variability during the New Zealand LOGS (including a middle LOGS warming phase) is corroborated by records that are emerging from West Coast sites (e.g. Hormes et al., 2003; Suggate and Almond, 2005; Vandergoes et al., 2005) and the Auckland maar records from the North Island (Sandiford et al., 2001, 2003; Hägg and Augustinus, 2003). Barrows and Juggins (2005) report that the greatest amount of SST cooling (⩽9 °C) off the east coast of New Zealand did not occur until the LGM (20,500±1400 cal yr BP (Fig. 4)). $\delta^{18}O$ records from the Md3 Nettle bed speleothem (Hellstrom et al., 1998) indicate a $\delta^{18}O$ minimum at about the same time as the SST minimum reported by Barrows and Juggins (2005) (Fig. 4). The timing of the largest peak in the abundance of grass pollen in the Okarito Pakihi pollen record (Vandergoes et al., 2005) also coincides with the timespan for the LGM as defined by EPILOG (2001) (Fig. 4). Marra et al. (2004) also performed temperature reconstructions based on beetle fossils from a samples ranging from ~22,900 to 24,600 cal yr BP from the Awatere Valley in the South Island (Figs. 1 and 4). Marra et al. (2004) inferred a maximum temperature decline of ca 5 °C for February and 6 °C for July mean temperatures from this site. Therefore, it appears that even though a series of glacial advances began in New Zealand ~34,000 cal yr BP, climate conditions were variable and the maximum cooling did not occur until much later until the LGM.

Many of the pollen records spanning the early part of the LOGS show a climate amelioration shortly after the deposition of the Kawakawa tephra (~26,500 cal yr BP) (Vandergoes et al., 2005). However, the continued low values (<20%) of canopy tree pollen (e.g. *Nothofagus*, *Dacrydium cupressinum*, *Podocarpus* spp.) (Moar, 1980; McGlone, 1988; Vandergoes et al., 2005) for the entire LOGS are seemingly at odds with the mild degree of cooling now inferred from the chironomids (this study) and the beetles (Marra et al, 2006) from Lyndon Stream for the middle of the LOGS.

Allowing for the maximum estimated cooling from Lyndon Stream (3.7 °C) (this study) and a lapse rate of 0.6±0.1 °C/100 m (Hales and Roering, 2005), the tree-line should drop from its present altitude (~1300 m) to ~680 m asl between 26,600 and 24,500 cal BP. Therefore large areas of the South Island should have been forested between ~27,000 and 23,000 cal yr BP. The fact that forest canopy trees remained sparse during the early LOGS suggests that some other environmental factors must have been limiting the growth of forest taxa during this period.

The Lyndon Stream record represents a time period of up to 2000 years. It is possible that a climate amelioration of such a short duration would not allow enough time for the regeneration of the forest cover. However, at the end of the last ice age (~18,000 cal yr BP) the pollen record shows a rapid recovery in the regional vegetation in response to climate change. McGlone et al. (2004) report that the native canopy tree pollen (*Nothofagus*/*Podocarpus*) from Kettlehole Bog (30 km north of the Lyndon Sream site (Fig. 1)) had reached an abundance of 45% within a thousand years of the last deglaciation.

The chironomids are only capable of reconstructing mean February temperatures, and it is likely that changes in seasonality, mean annual temperature (MAT) and frost frequency may exert a stronger control on vegetation cover rather than reduction in the summer temperature alone. The beetle-based MCR technique is also capable of reconstructing mean July (winter) temperatures (Marra et al., 2006). So far the beetle-based mean July temperature reconstructions from Lyndon Stream (Marra et al., 2006) show no significant change in seasonality during this time, with an equal amount of cooling (~2 °C) occurring in winter and summer. Further studies investigating the relationship between modern New Zealand pollen assemblages and environmental parameters are required to disentangle the environmental signals represented in the pollen record.

6. Conclusions

The mild (<4 °C) cooling for the late Otiran glacial sequence between ~26,600 and 24,500 cal yr BP (MIS 3/2

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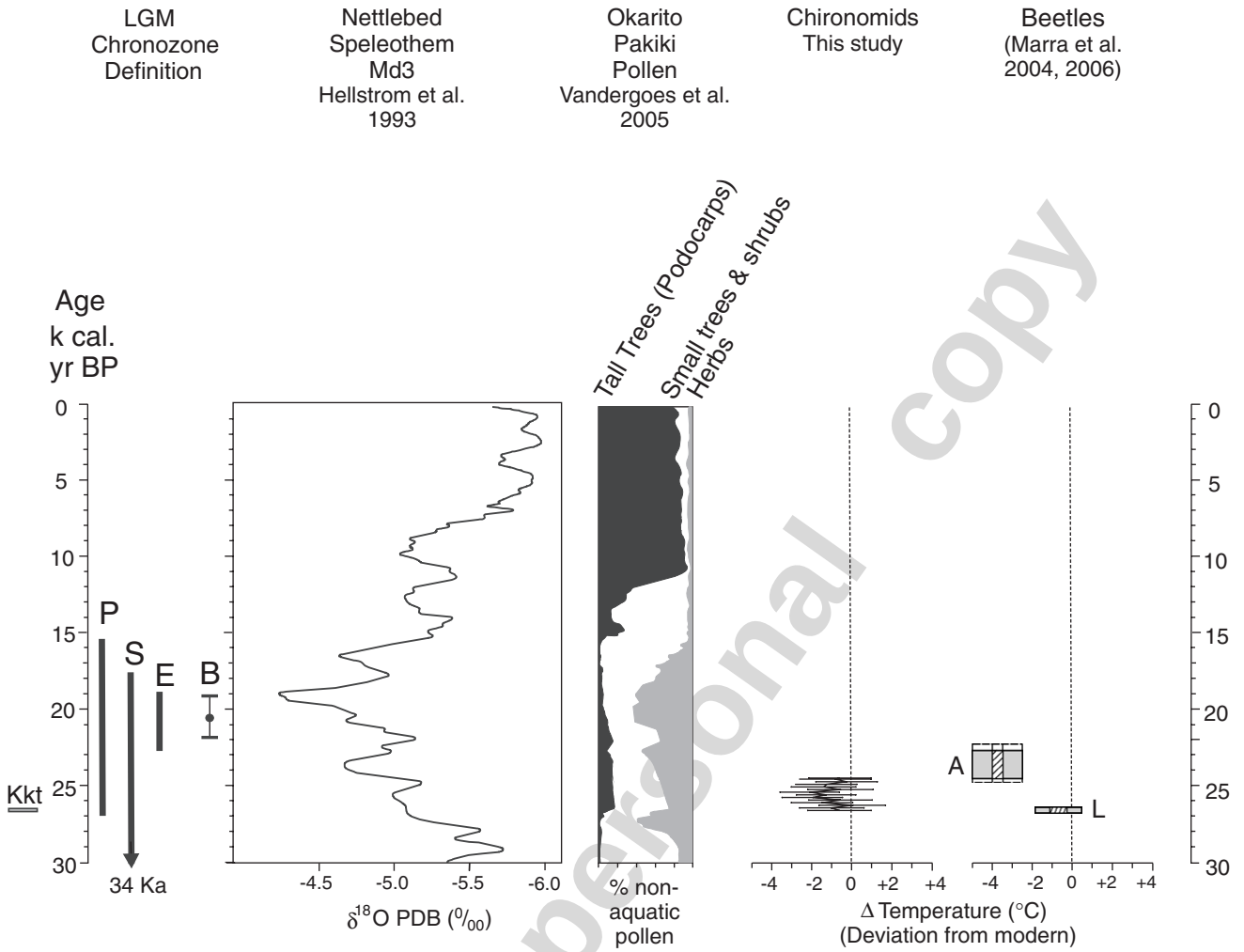

Fig. 4. The Lyndon Stream chironomid temperature record placed in context with other paleoclimate proxies. References are provided for each record. LGM definitions for New Zealand. P= Pillans et al., 1993; S= Suggate and Almond, 2005. E= the global LGM (EPILOG, 2001). B= the sea surface temperature minimum found in LGM records by Barrows and Juggins (2005). Abbreviations for beetle reconstructions: A= Awatere Valley (Marra et al., 2004), L= Lyndon Stream (Marra et al., 2006). Beetle-based February mean reconstructions are shown to allow a direct comparison with the chironomid temperature estimates.

transition) inferred from chironomids in this study is in agreement with the previous estimates by Soons and Burrows (1978) and the beetle-based estimates of Marra et al. (2006) from the same site. A period of climate amelioration (an interstadial) around this time is supported by other records emerging from other parts of New Zealand (Hormes et al., 2003; Suggate and Almond, 2005; Vandergoes et al., 2005) which indicate ice retreat and a slight recovery in the forest cover.

The apparent inconsistency between the pollen record and the mild conditions inferred from chironomids (this study) and beetles (Marra et al., 2006) during parts of the LGM requires further investigation. The pollen record does show a slight recovery coinciding with the late MIS 3 early MIS 2 'interstadial' but canopy tree pollen is still rare. This fact suggests that environmental parameters additional to temperature are contributing to limit the expansion forest cover during this time. This study highlights the potential of chironomids-based reconstructions to extend and amplify the late Quaternary paleoclimate history of New Zealand.

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